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Historical and taxonomic studies in the genus *Titanoderma* (Rhodophyta, Corallinales) in the British Isles

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CONTENTS

Introduction 2
Material and methods 2
Abbreviations 3
Thallus terminology 3
Taxonomic categories 4
Lectotypification 4
The history of *Titanoderma* 4
  Introduction 4
  E. J. C. Esper and J. B. Bory 4
  J. V. F. Lamouroux 5
  F. T. Kützing 5
  W. H. Harvey 5
  J. E. Areschoug 5
  C. Nägeli 5
  P.-L. and H.-M. Crouan 5
  S. M. Rosanoff 7
  M. P. Hariot 8
  F. Heydrich 8
  M. H. Foslie 9
  M. B. Nichols 10
  M. (Mme P.) Lemoine 10
  E. Y. Dawson 10
  H. Huvé 10
  T. Masaki and J. Tokida 10
  W. H. Adey 11
  J. Cabioch 11
  Wm. J. Woelkerling, Y. M. Chamberlain, and P. C. Silva 11
  Summary 11
Corallinales and Lithophylloideae 11
Titanoderma—basic features 13
  Spore segmentation 13
  Thallus structure and morphogenesis 13
  Reproduction 16
  Spermatangial plants 16
  Carpogonial/carposporangial plants 16
  Tetra/bisporangial plants 18
  Ecology 20
Titanoderma—taxonomy of British Isles plants 20
  Introduction 20
  Dimensions 20
  Colour 20
  Thallus characters 21
    Margin 21
    Imbrication 21
    Axial filaments 21
    Erect filaments 21
    Surface view 21
  Tetra/bisporangial conceptacles 21
    Conceptacle anatomy 21
    Conceptacle surface 21
  The organization of species descriptions 22

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Aids to identification 22
Principal substrata 22
Taxonomic descriptions 22
Titanoderma Naeg. 22
Key to *Titanoderma* in the British Isles 25
Field key to *Titanoderma* in the British Isles 25
1a. *Titanoderma pustulatum* (Lamouroux) Näg. var. *pustulatum* 26
1b. *Titanoderma pustulatum* var. *macrocarpum* (Rosanoff) Y. Chamberlain 33
1c. *Titanoderma pustulatum* var. *confine* (P. & H. Crouan) Y. Chamberlain 50
1d. *Titanoderma pustulatum* var. *canellatum* (Kütz.) Y. Chamberlain 61
2. *Titanoderma corallinae* (P. & H. Crouan) Woelkerling, Y. Chamberlain & P. Silva 66
3. *Titanoderma laminariae* (P. & H. Crouan) Y. Chamberlain 69
Glossary 76
Acknowledgements 76
References 77
Index 79

SYNOPSIS. *Titanoderma* Naeg. (syn. *Dermatolithon* Foslie) is a calcified, crustose red alga of the family Corallinaceae. An historical and taxonomic reassessment of the genus in the British Isles shows that it exhibits great variability making taxonomic differentiation difficult. Arising from this variability, and from the failure of previous authors to consult type specimens, considerable confusion is evident in the literature and no firm taxonomic basis has previously been established.

It is concluded that three species occur in the British Isles of which *Titanoderma corallinae* (P. & H. Crouan) Woelkerling, Y. Chamberlain & P. Silva and *T. laminariae* (P. & H. Crouan) Y. Chamberlain comb. nov. are well differentiated. The remaining published taxa have been subsumed in the very variable type species *T. pustulatum* (Lamouroux) Näg. However, four foci within a continuous matrix of variation in this species have been retained as varieties as follows: *T. pustulatum* (Lamouroux) Näg. var. *pustulatum, T. pustulatum* var. *macrocarpum* (Rosanoff) Y. Chamberlain comb. nov., *T. pustulatum* var. *confine* (P. & H. Crouan) Y. Chamberlain comb. nov., and *T. pustulatum* var. *canellatum* (Kütz.) Y. Chamberlain comb. nov.

Descriptions are given of the six above taxa based on British Isles material; relevant type and other historically important specimens are also described and seven previously published taxa are lectotypified.

INTRODUCTION

Although eight species of *Titanoderma* Naeg. (Corallinaceae, subfamily Lithophylloideae) have been recorded from the British Isles (Parke & Dixon, 1976, as *Dermatolithon* Foslie), a detailed account of the genus for this region has never been published and most records stem from general floristic surveys unsupported by data clarifying the structure and taxonomy of the plants concerned. As was found (Chamberlain, 1983) with the thin crustose genera *Fosliella* Howe and *Pneophyllum* Kützing, no reliable basis has been established for the classification of British Isles species of *Titanoderma* and no world monograph has yet been undertaken.

Recent studies by Chamberlain (1978*a*, 1986) and Woelkerling, Chamberlain & Silva (1985) have shown that current species concepts are not necessarily in accord with the type material and that the application of species names by some authors is incorrect. This paper, therefore, contains a taxonomic reassessment of the species of *Titanoderma* known to occur in the British Isles. The particular aims of the study have been: (1) to examine carefully the structure of *Titanoderma* plants found in the British Isles in order to establish reliable characters upon which the systematics of the group may be based; (2) to relate the species found in the British Isles to material from other regions (particularly from neighbouring parts of Europe), and also to relevant type specimens, in order to apply the correct species name in each case; and (3) to provide detailed descriptions and illustrations of British Isles material and type specimens in order to aid identification of local material and to establish data upon which later reassessment, on a world-wide scale, may be undertaken.

Species of *Titanoderma* are most frequently found as epiphytes on other algae and seagrasses, but they also commonly grow epilithically and epizoically. This study is based mainly on intertidal and subtidal collections made by myself and colleagues since 1975. Collections from many herbaria have been examined in the course of typification of relevant taxa, and material at BM, PC, TRH, and USNC has been studied in order to assess the few previous publications that have dealt with British Isles collections of *Titanoderma* in any detail, namely those by Foslie (1905*a*, etc.), Lemoine (1913*b*), Newton (1931), and Adey & Adey (1973). It has been found, however, that taxon delimitation is still far from easy. The difficulty may lie to some extent with the fact that the majority of British Isles material is bisporangial and therefore, presumably, apomictic. In addition, the occurrence of some species is limited to one or two plants at a time, and even these are often evident only on taking stones or host plants back to the laboratory. This study must, therefore, be regarded as preliminary; as Turrill (1952) said, when addressing phycologists: 'we have to accept for immediate use the most satisfying classification we can prepare and improve it in the course of use'.

The study starts with a description of relevant historical publications on *Titanoderma* which supplements a more general historical introduction given in Chamberlain (1983: 297–318). A description of structure and reproduction in the genus follows, and finally the genus and three species, one with four varieties, occurring in the British Isles are described.

MATERIALS AND METHODS

This study is based mainly on specimens collected in the British Isles between 1975 and 1987. Type and other historically

important specimens have been examined in the herbaria mentioned below under 'Abbreviations'.

Routine sectioning for examination under an optical microscope was performed using an MSE Pelcool freezing microtome at a thickness of 10–25 μm. For this purpose thallus fragments (attached to the host if epiphytic) were decalcified by placing them in Perenyi's fluid (4 parts 10% nitric acid: 3 parts 90% ethanol: 3 parts 0.5% chromic acid) until bubbling ceased; this usually took less than 10 minutes in the British Isles species of *Titanoderma*. The thalli were then soaked in 80% ethanol for at least 15 minutes and sectioned in Hamilton's solution (1 gm gum arabic: 30 gm sucrose: 1 crystal of thymol: 100 ml aqua dest.). The sections were transferred with a fine paint brush to a solution of 33% glycerine coloured with lactophenol cotton blue on a microscope slide. The mountant was allowed to evaporate gradually over two to three days; eventually the remaining glycerine was drained off and the thalli mounted in glycerine jelly coloured with crystal violet (see also Chamberlain, 1983: 295). Some sections were stained with 1–5% aniline blue and mounted in 60–80% Karo.

I am very grateful to Stuart Campbell who made resin-embedded sections for my use, employing the technique described in Woelkerling (1988: 34).

Dried thalli were used for scanning electron microscopy. They were briefly rinsed in distilled water to remove sodium chloride, then re-dried and lightly brushed. Thallus fragments were either mounted whole for surface features, or fractured using a sharp razor blade. Specimens were mounted on stubs using double-sided 3M Scotch tape and coated with gold/palladium in a Polaron E5000 sputter coater at 1.2 kV for 2–6 minutes. Specimens were examined in a Jeol T20 scanning electron microscope at 20 kV.

Most of the British Isles specimens mentioned specifically either in the text or plates (as 86/305 etc.) have been deposited in BM; a few were entirely used for microscopic preparations. Further specimens have also been deposited in BM or are retained by the author at present.

ABBREVIATIONS

Herbaria:

BM = Natural History Museum, London
BM-K = Royal Botanic Gardens, Kew (algae now amalgamated with BM collection)
C = Botanical Museum, Copenhagen
CHE = Société des Sciences Naturelles et Mathématiques de Cherbourg
CN = Université de Caen
CO = Laboratoire Maritime, Concarneau
FR = Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt
L = Rijksherbarium, Leiden
PC = Muséum National d'Histoire Naturelle, Paris (Cryptogams)
TRH = Kongelige Norske Videnskabers Selskab Museet, Trondheim (= Nidros)
UC = Botanic Herbarium, University of California, Berkeley
USNC = United States National Museum Coralline Collection, Washington, D.C.

Other abbreviations:

87/148 = Y. M. Chamberlain collection numbers (cited in captions etc.)
VS = vertical section
! = specimen seen
SEM = scanning electron microscope/microscopy/micrograph
tetra/bisporangial = in most respects, the taxonomic characteristics of tetrasporangial and bisporangial conceptacles are comparable. To save repetition therefore, the term tetra/bisporangial is used when neither one nor the other is being specified.

THALLUS TERMINOLOGY

The dorsiventral, crustose coralline thallus has traditionally been perceived as comprising a lower, uni- or multistratose layer of horizontally orientated filaments termed the hypothallium, and an upper layer of vertically orientated filaments, the perithallium (see Chamberlain, 1978*b*). An uppermost layer of non- or slightly calcified cells also occurs and is known as the epithallium.

Cabioch (1972) studied spore germination in crustose coralline algae and noted that in *Lithophyllum* a single layer of basal filaments (hypothallus) grew peripherally from the germinating spore and persisted, at least in the juvenile thallus, as the plant developed. In *Neogoniolithon* and *Lithothamnion*, in contrast, a multistratose basal layer (hypothallus) developed from the spore and persisted throughout the growing thallus. Recently Woelkerling & Irvine (in Woelkerling, 1988: 8) discussed the structure and morphogenesis of crustose coralline thalli with uni- and multistratose basal layers and proposed the terms 'dimerous' and 'monomerous' respectively to define them.

Woelkerling & Irvine (in Woelkerling, 1988: 259) also emphasized the importance of considering the thallus in terms of filament activity and proposed the following terminology for the components of the dimerous thallus: primigenous for the basal (hypothallial) filaments and postigenous for the upper (perithallial) filaments derived more or less at right angles from the primigenous filaments. They retained the term epithallial cells.

While I concur with Woelkerling & Irvine in recognizing two types of thallus, and agree with them in wishing to emphasize the filamentous nature of the thallus, I consider that the use of specialized terms such as hypothallium and perithallium has done a disservice to our understanding of crustose coralline algae. The terms have suggested that corallines are unrelated to other red algae, and this has possibly inhibited people from taking an interest in the group. The coining of further terms, exclusive to the Corallinales, to denote morphological structures that exist elsewhere in the red algae may serve to increase this isolation. I appreciate, however, that such terms may have their place in specialized literature.

In this study I propose to use the following adjectives for the filaments of the dimerous thallus: 'axial' for for the basal (hypothallial, primigenous) filaments and 'erect' for the vertical (perithallial, postigenous) filaments derived at right angles from them (Figs 9–11). The term axis is defined by Woelkerling (1988: 225) in one sense as 'a major line of growth from which

branches can arise'. I interpret the radiating basal filaments of the crustose thallus as axial in this sense and regard the erect filaments as lateral branches. Development of lateral branches is restricted to the upper surface of axial filaments as a consequence of the crustose growth habit. In genera such as *Metamastophora* (Woelkerling, 1988) where the axial filaments are upright and may give rise to lateral branches in more than one direction, the adjective 'lateral' rather than erect would be more appropriate.

I agree with Cabioch and Woelkerling & Irvine in retaining the adjective 'epithallial' for the mainly uncalcified cells that terminate most erect filaments. These cells are restricted to the Corallinales.

TAXONOMIC CATEGORIES

The background

Two infrageneric categories in particular have traditionally been applied in nongeniculate coralline algae: the species and the forma. Most taxonomists would probably agree that 'the species is for most purposes widely accepted as the basic unit of taxonomy' (Davis & Heywood, 1963: 89), although no definition of a species could be devised that would be acceptable to all taxonomists and infraspecific categories are even more controversial. The practice, within nongeniculate coralline algae, of applying forma to all variants, whether of a morphological, anatomical or geographical character, became accepted practice with Foslie (see Woelkerling, 1984) and was to some extent followed in the works of Lemoine (see Ardré & Cabioch, 1985; Chamberlain, 1985*b*).

Recent studies

The precedent set by Foslie has led to the establishment of a large number of specific and infraspecific taxa that are, for the most part, poorly delimited, and more recent studies suggest that a considerable reduction in the number of such taxa will occur. Woelkerling (1980), for example, considers that all published species of *Metamastophora* should be accommodated within *M. flabellata* (Sonder) Setch. It is also suggested by Adey et al. (1982) that 'pair species', occurring in the Atlantic and Pacific Oceans, may prove to be conspecific, although the authors have chosen to maintain their separation as an intermediate solution until unequivocal evidence is available to support their combination.

Proposed categories

While I have been investigating *Titanoderma* in the British Isles, Dr Wm J. Woelkerling and Mr S.J.Campbell have been studying the genus in southern Australia and we have jointly concluded that certain species, such as *T. pustulatum,* are highly variable. In European populations of *T. pustulatum*, however, there are four morphological focal points within the matrix of variation (see pp. 20, 23, 25) that merit formal infraspecific denomination at the rank of variety. Both Davis & Heywood (1963) and van Steenis (1958) suggest that subspecies and variety have geographical connotations, but it is possible that marine algal taxonomy has to be considered in a different light from angiosperm taxonomy because distributional barriers are so different. Lawrence (1951: 55–56), however, suggests definitions of both subspecies and variety that do not have geographical connotations. As a result of discussions involving Wm J. Woelkerling, S. J. Campbell, and myself, it was concluded that Lawrence's approach was the most appropriate and that ranks of subspecies and variety be applied in the following manner:

SUBSPECIES. For cases where available evidence suggests that two or more species may be represented but which at present cannot be unequivocally separated. Such subspecies are to be delimited on morphological/anatomical grounds without consideration of geographical distribution (which is inadequately known) or genetic characteristics (which are unknown).

VARIETY. For cases where it is desirable or advantageous formally to name particular morphological/anatomical focal points within a highly and continously variable species. No geographic or genetic bases are assumed or implied.

LECTOTYPIFICATION

1. Taxa now included in *Titanoderma pustulatum*
Lectotypes have been chosen for:
Melobesia hapalidioides P. & H. Crouan, p. 36
Melobesia simulans P. & H. Crouan, p. 40
Melobesia confinis P. & H. Crouan, p. 53
Lithophyllum macrocarpum f. *faeroensis*, p. 26.
Lithophyllum pustulatum f. *intermedia* Foslie, p. 53
Melobesia pustulata β *canellata* Kütz., p. 61

2. Species now named *Titanoderma corallinae*
A lectotype has been chosen for:
Melobesia corallinae P. & H. Crouan, p. 66

3. Species now named *Titanoderma laminariae*
A lectotype has been chosen for:
Melobesia laminariae P. & H. Crouan, p. 70

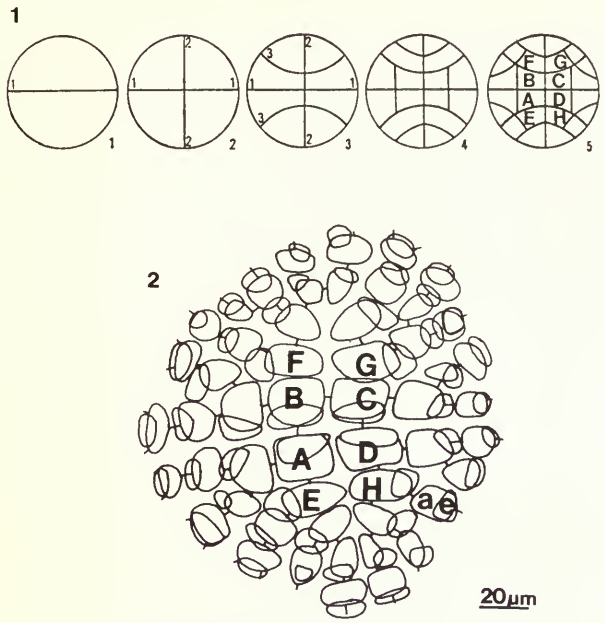
THE HISTORY OF *TITANODERMA*

Introduction

The nomenclatural and taxonomic history of *Titanoderma, Tenarea, Fosliella, Pneophyllum*, and *Melobesia* are interwoven, as indicated by Chamberlain (1983, table 1), by Woelkerling, Chamberlain & Silva (1985), and in the following notes (see Esper, Bory, Foslie, Hariot, and Lemoine in particular).

E. J. C. Esper and J. B. Bory

Esper (1796: 118, *Millepora* pl.xxii) described *Millepora tortuosa*, a globular, calcareous organism from the Mediterranean, composed of a dense mass of twisting lamellae. This species was later re-described by Bory (1832) on the basis of plants (PC!) collected at Cape Tainaron on the Mediterranean shore of Greece. Bory erected the new genus *Tenarea* to accommodate Esper's plant, which he considered to be conspecific with his own material, and at the same time changed its specific name to *undulosa*, presumably because, as he remarked, Esper had used the epithet *tortuosa* for



Figs 1–2 Spore germination in *Titanoderma*.
1. Stages in *Titanoderma* spore germination redrawn after Notoya (1974). Numbers indicate successive planes of division, letters correlate with positions in Figs 1 and 2.
2. Drawing of centre of *T. pustulatum* var. *pustulatum* sporeling in Fig. 4 showing epithallial cells (e) overlying axial filament cells (a), lines connecting axial cells represent primary pit connections.

another organism (illustrated on his plate xxv) as well. Esper's specimen, on which the name *Tenarea* must be based, was not re-examined for 189 years (Woelkerling et al., 1985); meanwhile the name *Tenarea* was forgotton until revived by Hariot (1895) after which many authors discussed its possible identity.

J. V. F. Lamouroux

The first publication of some species now considered to belong to *Titanoderma* was made by Lamouroux (1812) when he described, as an animal, a new genus, *Melobesia*, and attributed to it the following three species: *M. membranacea* (the type of the genus, see Mason, 1953; Chamberlain, 1985*a*), *M. orbiculata*, and *M. verrucata*. The species were nomina nuda at this date, but later Lamouroux (1816) revised the generic description and four species were described: *M. membranacea, M. pustulata, M. farinosa,* and *M. verrucata.* Of these *M. pustulata* and *M. verrucata* are now classified in *Titanoderma* and *M. pustulata* was designated type species of the genus *Titanoderma* by Nägeli (1858) and *Dermatolithon* by Foslie (1898*b*). *Melobesia verrucata* was at first recognized as a distinct species (Kützing, 1843 et seq.; Harvey, 1849; Areschoug, 1852; Crouan & Crouan, 1867) but Rosanoff (1866) subsumed it in *M. pustulata.* It was recently re-established as a species (Chamberlain, 1986) but it is now subsumed in *Titanoderma pustulatum* var. *canellatum*.

F. T. Kützing

Kützing (1841: 30; 1843: 385, pl. 78, fig. 1) described and figured *Melobesia* as characteristically having elongated basal thallus cells and it is evident, as discussed previously (Chamberlain, 1983: 299), that his concept of the genus corresponds with the current concept of *Titanoderma*. Examination of Kützing's herbarium specimens (L) of *Melobesia* spp. mainly confirms this hypothesis although other genera, particularly *Fosliella*, were also included in *Melobesia*. The main points regarding species identification that emerge from studying Kützing's specimens are:
(1). His concept of *M. verrucata* is a foraminiferan;
(2). His concept of *M. pustulata* includes *Titanoderma pustulatum* var. *macrocarpum,* var. *canellatum,* and *Fosliella* spp.;
(3). His concept of *M. membranacea* is var. *canellatum;*
(4). His new form *M. pustulata* β *canellata* is var. *canellatum*.

It is interesting that two of Kützing's specimens were annotated by Foslie, who also applied the name (*Dermatolithon*) *pustulatum* to plants that would now be identified as var. *canellatum*.

W. H. Harvey

Corallines were omitted from Harvey's (1841) *Manual of British algae*, presumably because he regarded them as animals at this time. In his subsequent publication *A manual of the British marine algae* (Harvey, 1849: 104) he commented that the corallines had until recently been considered as zoophytes or corals but that their plant-like nature had now become widely accepted. Two species attributable to *Titanoderma* were included by Harvey (1849, 1851) in the genus *Melobesia*. These were *M. pustulata* and *M. verrucata.* Harvey's records were subsequently widely referred to (e.g. Areschoug, 1852; Rosanoff, 1866) but unfortunately it has proved impossible so far to locate Harvey's specimens and his illustrations are not sufficiently detailed to enable secure identification of the species to hand.

J. E. Areschoug

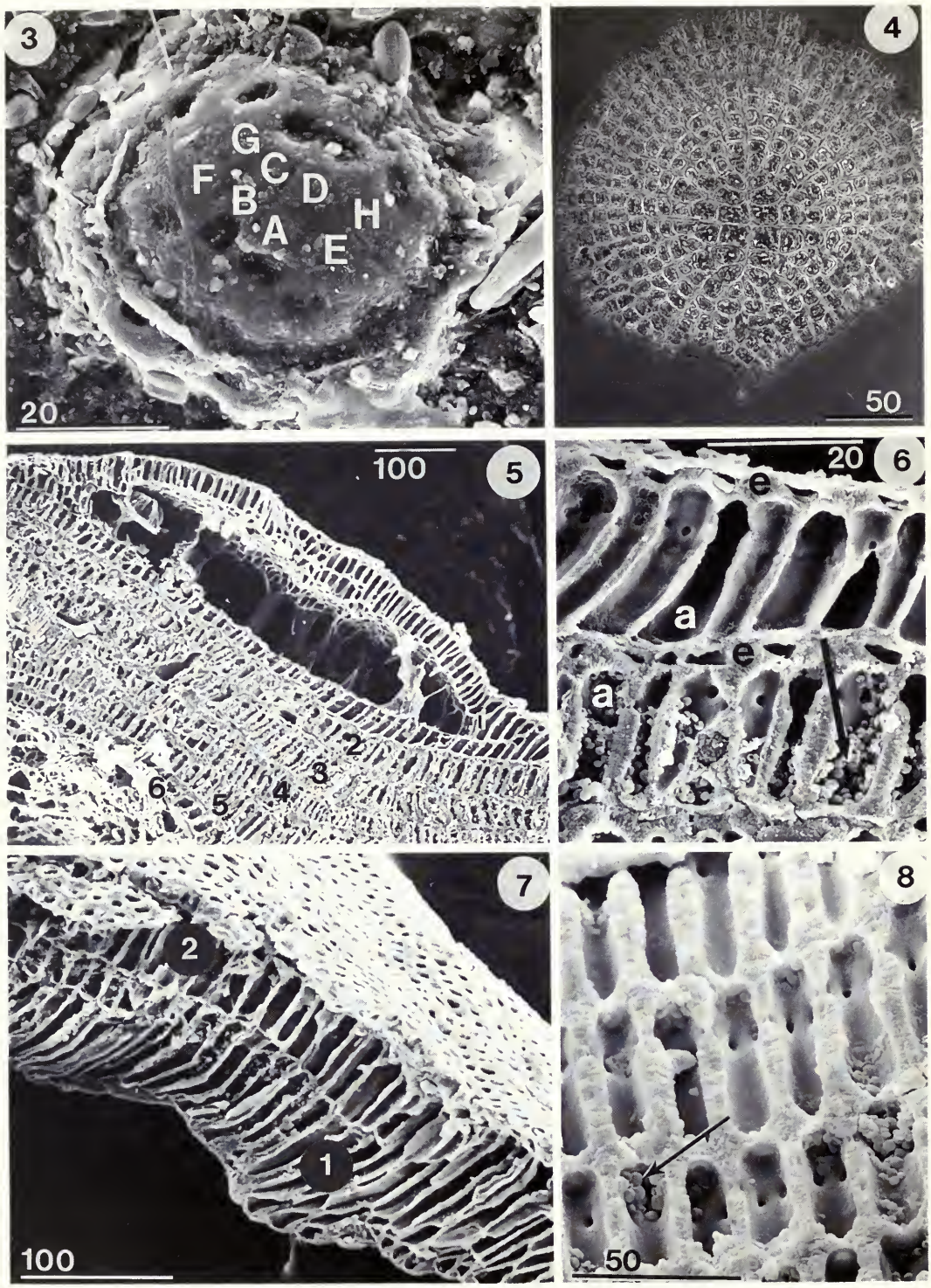
Areschoug (1852) followed Kützing (1843, 1849) and Harvey (1849) in recording *M. pustulata* and *M. verrucata* as representing a larger and smaller species of *Titanoderma*.

C. Nägeli

Nägeli (1858), in a footnote, erected the genus *Titanoderma* to accommodate Lamouroux's *Melobesia pustulata* which he said had two-celled sporangia as opposed to the four-celled sporangia of true *Melobesia*.

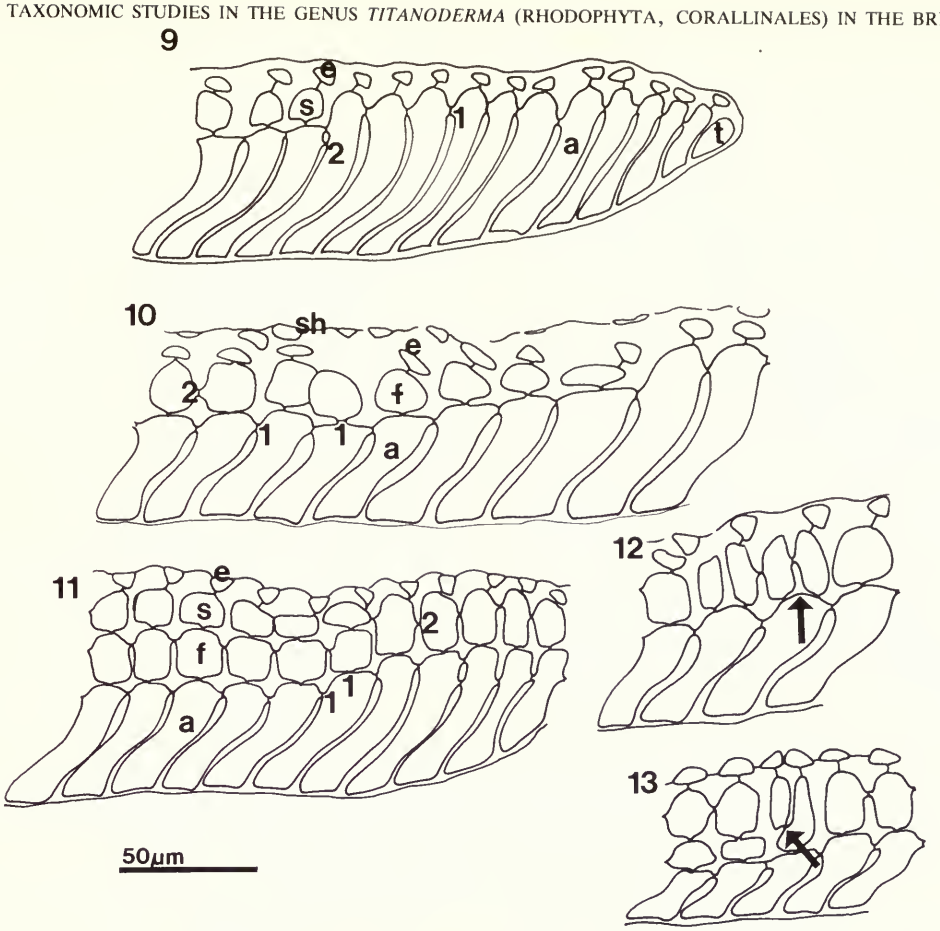
P.-L. and H.-M. Crouan

As commented previously (Chamberlain, 1983: 301), the work of the Crouan brothers is of particular importance in respect to the simple, nongeniculate corallines as they were among the earliest authors to devote attention to these taxa. After listing them without descriptions (Crouan & Crouan, 1860), the Crouans (1867) described seven species of *Titanoderma* (as *Melobesia*) of which only *M. pustulata* and *M. verrucata* had previously been recorded. Examination of their herbarium (CO) shows, however, that smaller plants identified as *M. verrucata* were mainly *Fosliella* as was found also with Kützing's (L) material. Their *M. pustulata* specimens, on the other hand, pertain to the type variety of *T. pustulatum*. Two of the Crouans' new species, *M. corallinae* and *M. confinis*, were mainly epiphytic on *Corallina*; two of them, *M.*



Figs 3–8 Spore germination and thallus features of *Titanoderma* (scales in μm).

3. Sporeling of *T. corallinae*, compare with Figs 1 and 2 for location of cells A–H.
4. Sporeling of *T. pustulatum* var. *pustulatum* (84/286) under phase contrast, orientation as in Fig. 2.
5. Vertical fracture of type specimen (TRH) of *T. prototypum* showing a conceptacle in the uppermost layer of thallus (1) above five further thallus layers (2–5).
6. Detail from Fig. 5 showing two thallus layers with successive epithallial (e) and axial (a) cells, starch grains (arrow) are present.
7. Vertical fracture of *T. pustulatum* var. *pustulatum* (84/146) showing relatively light calcification of axial (1) and erect filament (2) cells.
8. Vertical fracture of erect filament cells of type (CO) specimen of *Melobesia hapalidioides* (= *T. pustulatum* var. *macrocarpum*) showing heavy calcification of side walls, starch (arrow) is present.



Figs 9–13 Vertical sections to show thallus features of *Titanoderma* (thallus edge to right in all sections).

9. Thallus margin of *T. pustulatum* var. *pustulatum* (75/143) showing terminal initial giving rise to axial filament with cells which bear triangular epithallial cells. The axial cells later divide to initiate erect filaments.

10. Thallus of var. *pustulatum* (84/59) in which erect filaments are initiated from axial cells with the primary pit connection remaining in the axial filament. A secondary pit connection later develops between contiguous cells of erect filaments. Old epithallial cells are being shed from the surface.

11. Thallus of lectotype specimen of *Melobesia macrocarpa* (= *T. pustulatum* var. *macrocarpum)* showing the continued growth of erect filaments from the subepithallial initial.

12. Thallus of var. *pustulatum* (75/143) in which two axial cells cut off two erect filaments each (arrow). In this case only one of each pair has developed an epithallial cell.

13. Thallus of var. *pustulatum* (75/143) showing an erect filament cell dividing pseudodichotomously (arrow).

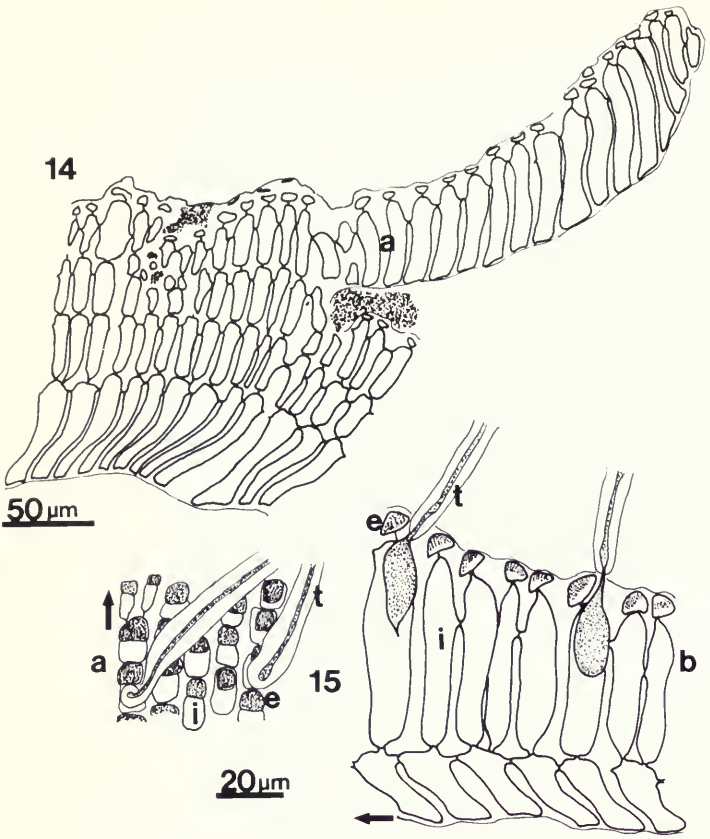
a = axial cell, f = erect filament cell, e = epithallial cell, s = subepithallial initial, sh = shedding epithallial cell, t = terminal initial, 1 = primary pit connection, 2 = secondary pit connection.

hapalidioides and *M. simulans,* grew on shells and porcelain; and the remaining species, *M. laminariae*, was epiphytic on *Laminaria digitata* stipes. As will be seen, examination of the Crouans' original material (CO and PC) shows that *M. corallinae* and *M. laminariae* are valid species while the other three species are now accommodated as varieties of *T. pustulatum*. Unfortunately failure by subsequent authors (especially Foslie, 1900*a*, etc.) to study the original material has led to many misapplications and much confusion in respect to the Crouans' species. As with *Pneophyllum* (Chamberlain, 1983), specimens at Concarneau have been chosen as lectotypes where possible. In the case of *M. confinis*, no specimen remains in CO and one in PC has been selected instead.

S. M. Rosanoff

Outstanding as his work was in many ways, Rosanoff's studies (1866) served to obfuscate rather than clarify previous conclusions regarding the naming of species of *Titanoderma*. Rosanoff went to Caen to study Lamouroux's herbarium (see Johnson & Hensman, 1899—quoted on p. 62 in the present study) and concluded that while *M. pustulata* was a good species, *M. verrucata* (Rosanoff, 1866: 78) simply represented the same species growing on the terete thallus of *'Rytiphloea'* as opposed to the flat fronds of *Chondrus*. Rosanoff (1866: 78) concluded that specimens recorded as *M. verrucata* by Areschoug, Kützing, and Harvey were either *M. membranacea* (Esper) Lamouroux or *M. farinosa* Lamouroux (*Fosliella*) but while this is, to some extent, true, the type of *M. verrucata* (Chamberlain, 1986) is now considered to be *T. pustulatum* var. *canellatum*.

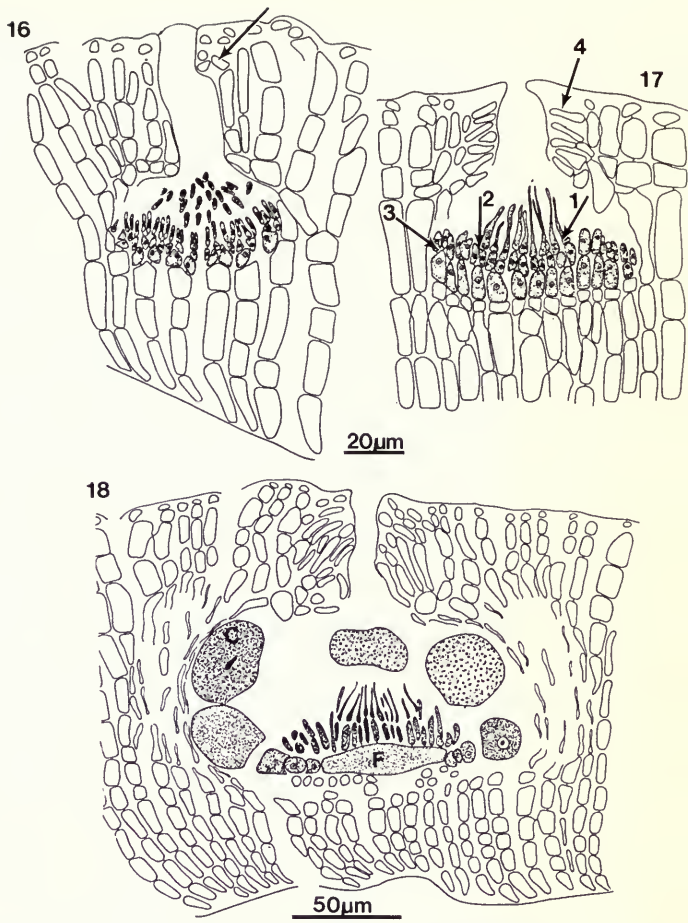
I examined the specimens (CHE) listed by Rosanoff (1866) as *M. pustulata* and found that, as with Kützing (q.v.), his concept of the species conformed to the smaller plants referrable to var. *canellatum*. He then went on to describe a new species, *M. macrocarpa*, to accommodate the larger



Figs 14–15 To show thallus features of *Titanoderma*

14. Vertical section of type specimen (PC) of *Melobesia confinis* (= *T. pustulatum* var. *confine*) to show regeneration of an axial filament (a).

15. Surface view (a) and vertical section (b) of *T. pustulatum* var. *confine* (87/62) to show the occurrence of trichocytes (t) originating in a small cell attached to the subepithallial initial (i), the trichocytes emerge through the layer of epithallial (e) cells, the arrows indicate the direction of the thallus edge.



Figs 16–18 Vertical sections of gametangial/carposporangial conceptacles of *Titanoderma corallinae* (reproduced from Suneson, 1943: figs 25, 26).

16. Spermatangial conceptacle showing spermatangial mother cells on the conceptacle floor which initiate elongate spermatangia from two loci. The spermatangia round off when released. Surrounding filaments grow to form the conceptacle roof (arrow).

17. Carpogonial conceptacle with central supporting cells bearing two carpogonia with trichogynes (1), or a carpogonium and a sterile branch (2). Sterile branches (3) occur peripherally. Surrounding filaments grow to form the conceptacle roof (4).

18. Carposporangial conceptacle with a central fusion cell (F) that initiates gonimoblast filaments with terminal carposporangia (C) peripherally. Old carpogonia and sterile branches persist on the surface.

forms. Examination of the type (CHE, see Chamberlain, 1986) reveals that this is a distinct variety strongly resembling var. *pustulatum* externally but anatomically distinct. It is now recombined as *T. pustulatum* var. *macrocarpum*. Unfortunately Foslie's (1900*a*, 1905*a*, etc.) difficulties in characterizing *pustulatum* and *macrocarpum* resulted in their becoming nomenclaturally inextricable.

M. P. Hariot

Bory's genus *Tenarea* was ignored until Hariot (1895) re-examined Bory's specimen (PC) and concluded that it was a nongeniculate coralline alga. Despite noting that Bory (1832) referred to *Millepora tortuosa* Esper, Hariot chose to use the epithet *undulosa*. Hariot concluded that *Tenarea* Bory (1832) was congeneric with *Lithophyllum* Philippi (1837) but only Kuntze (1898: 433) of subsequent authors adopted the older name for the genus recognized as *Lithophyllum*.

F. Heydrich

Initially Heydrich (1897*a*) recognized the genus *Melobesia* Lamouroux as including 10 species among which were Lamouroux's *M. membranacea* and *M. pustulata*. Shortly afterwards (Heydrich, 1897*b*) he erected the new genus *Epilithon*, into which he transferred *M. membranacea* on the basis that its tetrasporangia were borne in sori (i.e. were multiporate) rather than in conceptacles. However, *Melobesia* Lamouroux must be typified with *M. membranacea* (see Mason, 1953: 319, 320) and, therefore, by his exclusion of the type species Heydrich (1897*b*) created the later, illegitimate homonym *Melobesia* Heydrich (see Greuter, 1988, Art. 48.1). Although Heydrich (1897*b*) did not designate a type, Foslie (1898*a*: 16) briefly recognized *Melobesia* sensu Heydrich and designated *M. pustulata* Lamouroux as type species by which act *Melobesia* Heydrich became a homotypic synonym of *Titanoderma*. Later Foslie (1898*b*) accommodated *M. pustulata* in a newly erected genus, *Dermatolithon*, which thus

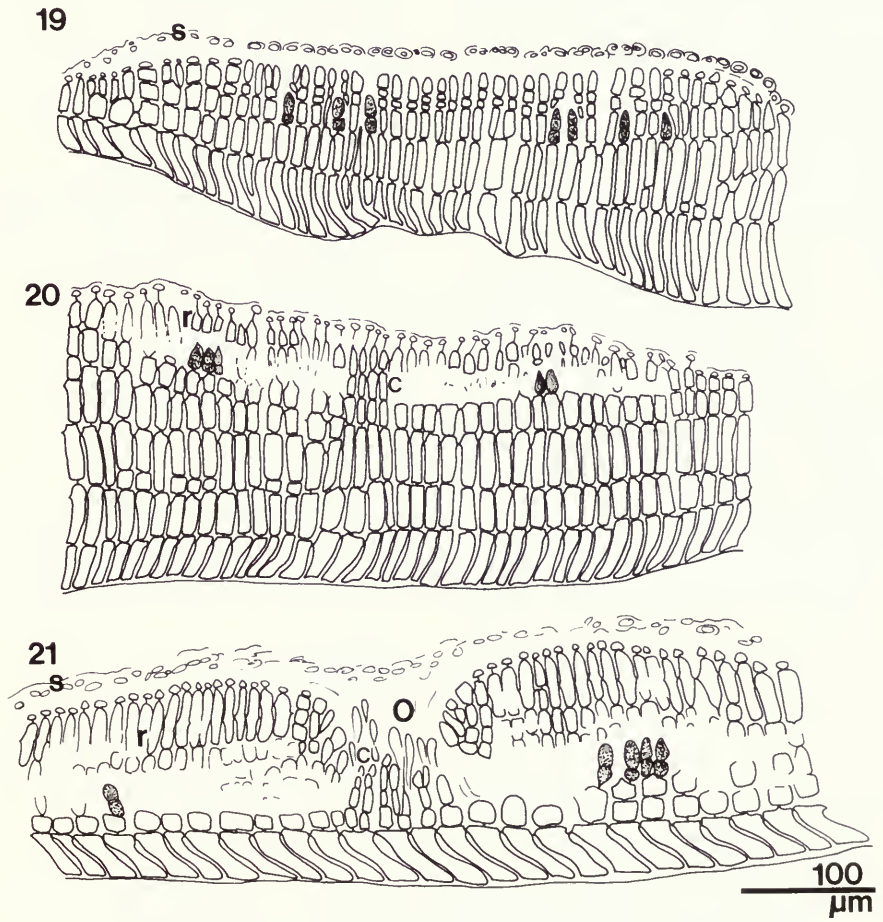
became a homotypic synonym of *Melobesia* Heydrich and *Titanoderma*.

M. H. Foslie

As Woelkerling (1984) ruefully remarked, 'With respect to the specific and infraspecific taxonomy of nongeniculate Corallinaceae, there is little doubt that the publications of M. H. Foslie have created more difficulties than those of nearly any other author'. The reasons were many, but principally Foslie based labryrinthic descriptions on minimal evidence, he did not illustrate the anatomical features of the material he described, he either failed to examine previous authors' type material or did so inadequately, and he published his changes of mind with great frequency. Foslie was continually being sent collections of corallines from all over the world and his efforts to process the material rapidly probably account for the rather superficial and inadequate nature of his descriptions. Fortunately his specimens are carefully preserved and readily accessible thanks to the ever-patient co-operation of the present curator of the Trondheim herbarium, Dr S. Sivertsen.

A synopsis of relevant information regarding Foslie's schemes of classification (Foslie, 1898*a*, 1898*b*, 1900*b*, 1905*a*, 1905*b*) is set out in Chamberlain (1983, tables 3, 4). Foslie (1898*a*) initially maintained *pustulata* Lamouroux in *Melobesia* sensu Heydrich, the genus he characterized at that date as having a single orifice (i.e. tetra/bisporangial ostiole) with paraphyses (presumably columella). Later the same year, Foslie (1898*b*) changed the circumscription of *Melobesia* to a 'single orifice, no paraphyses' (including mainly species now attributable to *Fosliella* and *Pneophyllum*) and erected *Dermatolithon* to accommodate species with paraphyses; all the species he included would now be attributable to *Titanoderma*. Subsequently, Foslie (e.g. 1905*a*, 1905*b*; 1909: 46) reduced and retained *Dermatolithon* as a subgenus of *Lithophyllum*, but at the end of the latter paper (Foslie, 1909: 57) he reinstated *Dermatolithon* on the basis of the presence of a single basal layer of palisade-like axial (hypothallial) cells as opposed to the many, non-palisade, basal cell layers of *Lithophyllum*. This feature has been accepted ever since as the identifying character of *Dermatolithon* Foslie under various generic names. Foslie did not know about the publication of *Titanoderma* Nägeli (1858).

Foslie (1905*a*) established *Litholepis* for three species of nongeniculate coralline algae but failed to designate a type



Figs 19–21 Vertical sections of *Titanoderma pustulatum* var. *pustulatum* showing early stages in the development of bisporangial conceptacles.

19. Specimen 83/225A showing young bisporangia (shaded) which have recently been initiated and have already differentiated into stalk cell below and sporangial initial. Erect filaments are starting to grow up round them and the epithallial cells are being shed (s).

20. Specimen 75/143 showing further growth of surrounding erect filaments which are splitting to produce young roof cells (r) above. The columella (c) is forming.

21. Specimen 84/99 showing further roof formation (r); the columella (c) is retracting to initiate the development of the ostiole (o), further epithallial shedding (s) is taking place. The walls of some roof cells have disintegrated.

species. Subsequently Hamel & Lemoine (1953: 109) lectotypified *Litholepis* with *L. caspica* (Foslie) Foslie which Woelkerling (1986) later showed to be a species of *Titanoderma*. Woelkerling (1986), therefore, concluded that *Litholepis* Foslie was a heterotypic synonym of *Titanoderma*.

Foslie's dealings with species and forms (Tables 2, p. 29, 3, p. 31) of *Titanoderma* are even more erratic than with the genus. Some of the resulting complexities are discussed in Chamberlain (1986) and in the descriptions of most of the taxa in the present investigation.

M. B. Nichols

Nichols (1909) described material of four forms of *Titanoderma* growing on the west coast of the United States of America, retaining them in *Lithophyllum*. Three forms pertain to *T. pustulatum* var. *confine* (q.v.), but *L. pustulatum* f. *australis* is a *Pneophyllum*.

M. (Mme P.) Lemoine

Lemoine (1912) recognized *Lithophyllum* subgenus *Dermatolithon* until 1953 (in Hamel & Lemoine, 1953) when she accepted *Dermatolithon* as an independent genus. In 1971, she published an assessment of recent species of *Dermatolithon*, grouping the species under various criteria.

Lemoine (1910, 1911) also studied the *Tenarea* problem (see Esper and Bory) in her early publications when, without examining anatomically either Esper's or Bory's plants of *Tenarea*, she concluded that:

a) they were the same taxon as the *Lithophyllum* that forms 'trottoirs' at the intertidal/subtidal interface in the western Mediterranean; and

b) that this 'trottoir' alga differed anatomically from true *Lithophyllum*.

Lemoine, therefore, applied the name *Tenarea tortuosa* to the 'trottoir' plant: this plant, however, is correctly named *Lithophyllum lichenoides* Philippi (Woelkerling et al., 1985).

E. Y. Dawson

Dawson (e.g. 1960) included species of *Dermatolithon* in many of his works; in 1955 he published a key to living species of the genus.

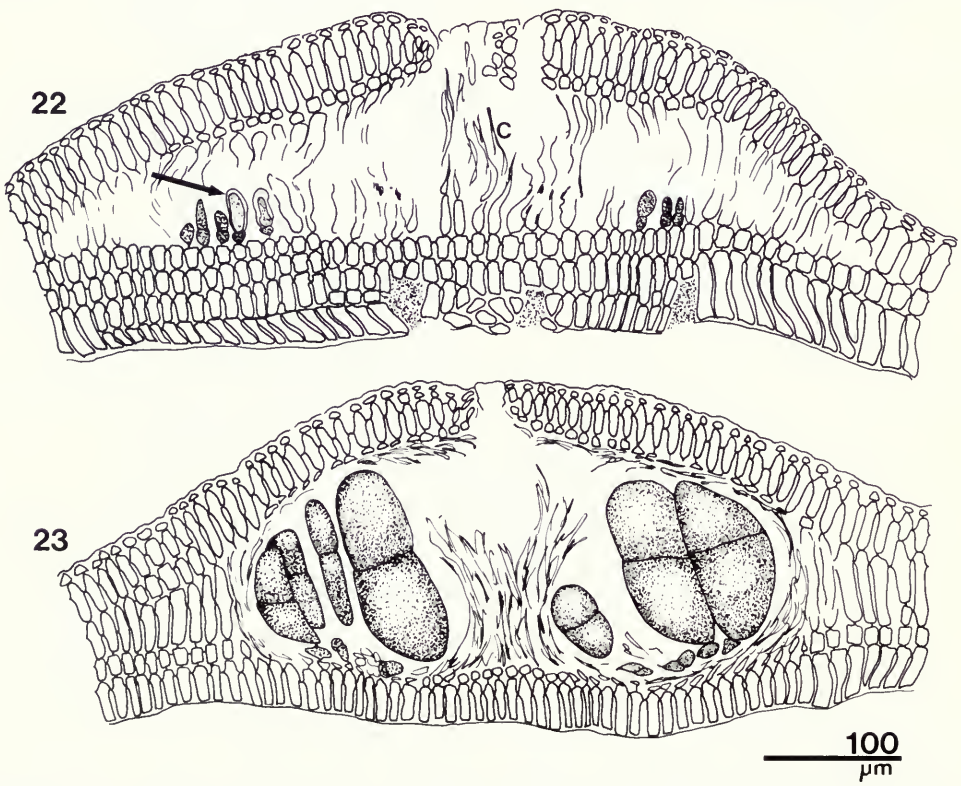
H. Huvé

In 1957, Huvé became the first author to re-examine the anatomy of Bory's type of *Tenarea undulosa* and she was able to show that the erect blades with their two opposed rows of cells resembling the oblique, palisade axial cells of *Titanoderma* (as *Dermatolithon*), were generically distinct from *Lithophyllum*. On the other hand she also showed that the 'trottoir' alga was a true *Lithophyllum* which she accepted as *L. tortuosum* (Esper) Foslie although she had not seen Esper's type of *Millepora tortuosa*.

Huvé also considered that the erect fronds and ventrally fused axial filaments of *Tenarea* were sufficient to distinguish it generically from *Titanoderma* which could, therefore, continue to be typified with *Melobesia pustulata* Lamouroux.

T. Masaki and J. Tokida

Tokida and his student Masaki published three papers that included descriptions and illustrations of four species of *Titanoderma* (as *Dermatolithon*) from Japan (Tokida &



Figs 22–23 Vertical sections of *Titanoderma pustulatum* var. *pustulatum* showing maturation of bisporangial conceptacles.
22. Specimen 85/30 in which the bisporangia are beginning to swell (arrow) and the roof and columella (c) are fully formed.
23. Specimen 85/30 showing a mature conceptacle with fully enlarged bisporangia.

Masaki, 1959; Masaki & Tokida, 1960*a*, 1960*b*) and subsequently Masaki (1968) included these species in his compendium of Japanese crustose corallines.

W. H. Adey

In a revision of the Lithophylleae, Adey (1965: 79) proposed that *Tenarea* Bory and *Dermatolithon* Foslie were congeneric; he considered that it would be preferable to adhere strictly to the rules of priority and he and a number of other authors (e.g. Adey, 1970; Littler, 1971; Adey & Adey, 1973; Johansen, 1976*a*, 1976*b*) have recognized *Tenarea* as the only lithophylloid genus with a single row of oblique, palisade, axial (hypothallial) cells.

J. Cabioch

Cabioch (1972, 1988) accepted *Titanoderma* (as *Dermatolithon*) as a distinct genus and examined and interpreted its vegetative structure in relation to other genera of Lithophylloideae.

Wm J. Woelkerling, Y. M. Chamberlain, and P. C. Silva

By a piece of good fortune, Woelkerling et al. (1985) finally discovered the type specimen of *Millepora tortuosa* Esper (FR!) and were able to establish that it was conspecific with specimens Bory (1832) referred to *Tenarea undulosa* Bory; the correct name for the taxon, therefore, becomes *T. tortuosa* (Esper) Lemoine. They also concluded that, as Huvé had suggested, *Tenarea* and *Dermatolithon* are distinct genera; however, an earlier generic name, *Titanoderma* Näg., was also typified with *Melobesia pustulata* and *Titanoderma*, therefore, has priority over *Dermatolithon*. Finally they concurred with Huvé that the 'trottoir' alga was a true *Lithophyllum* and they found that it was conspecific with *L. lichenoides* Philippi (Woelkerling, 1983).

The synonymy of *Tenarea* and *Titanoderma* is summarized in Woelkerling (1988: 106 and 111).

Summary

The conclusions arrived at are, therefore:

(1). *Titanoderma* (syn. *Dermatolithon*) is a nongeniculate, dorsiventrally organized lithophylloid genus with a single layer of oblique, palisade, axial cells. It may have a bistratose thallus, or erect filaments may develop. The type species is *Melobesia pustulata* Lamouroux which is now named *Titanoderma pustulatum* (Lamouroux) Näg.

(2). *Tenarea* is a nongeniculate lithophylloid genus with erect fronds composed of two layers of palisade axial cells arranged with their ventral surfaces in contact with one another. The type species is *Millepora tortuosa* Esper, which is now named *Tenarea tortuosa* (Esper) Lemoine.

(3). The 'trottoir' alga is a true *Lithophyllum* which is correctly named *L. lichenoides* Philippi.

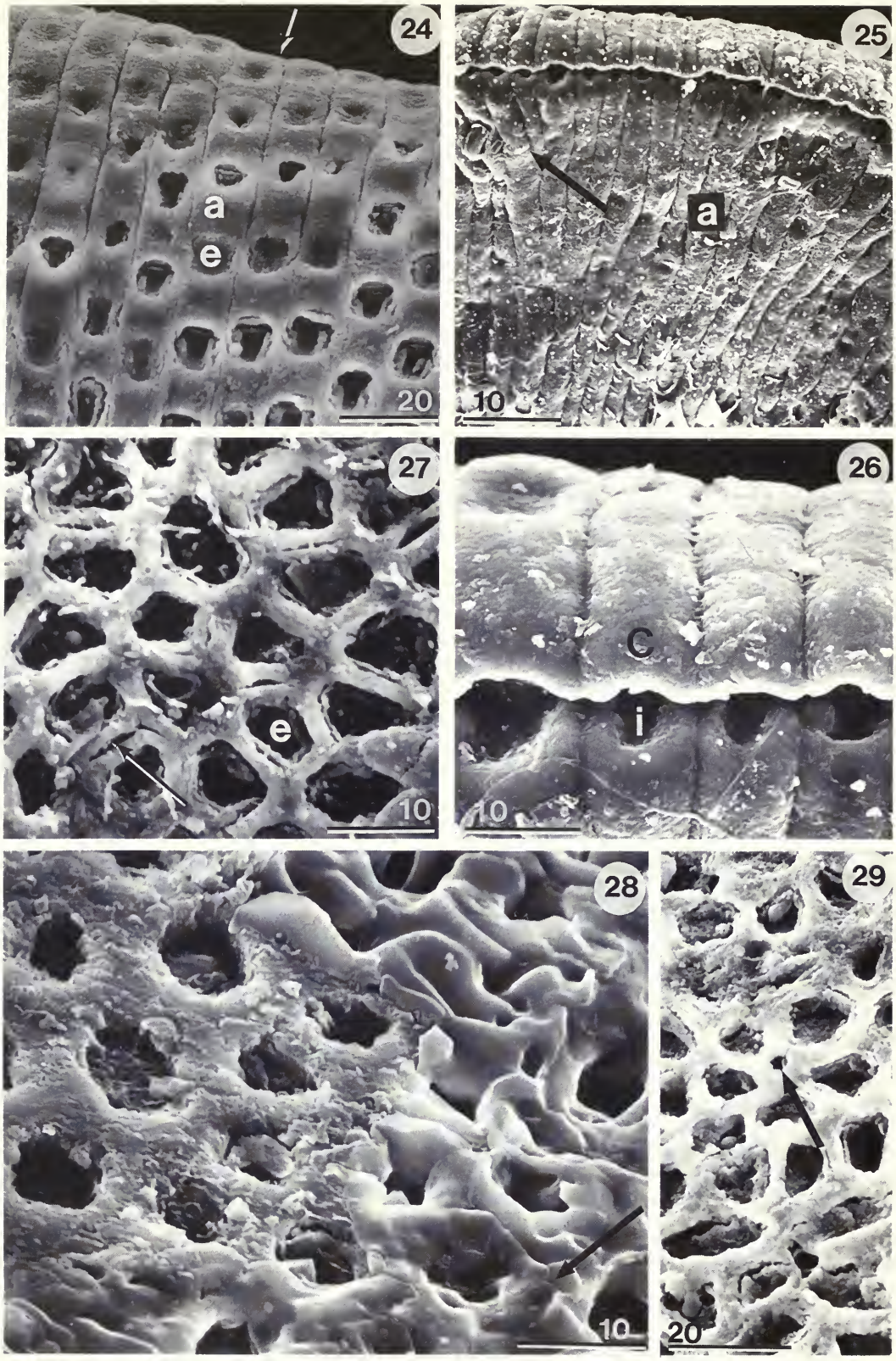
CORALLINALES AND LITHOPHYLLOIDES

In a recent publication Silva & Johansen (1986) validated the order Corallinales, thus legitimatizing a name which had already been used by various authors (e.g. Irvine, 1983). The principal distinguishing characters of the order are: (**1**) impregnation of the cell walls with calcite; (**2**) the common presence of intercalary meristems; (**3**) plugs of primary pit connections having two-layered, dome-shaped caps; (**4**) reproductive structures produced in roofed conceptacles (except *Sporolithon*); (**5**) tetrasporocytes usually undergoing simultaneous, zonate division; and (**6**) post-fertilization events involving a cluster of procarpial filament systems. The authors suggest further characters of secondary importance including the consistently occurring, two-celled carpogonial filaments; the prevalence of secondary lateral anastomoses; the occurrence of a self-perpetuating, presumably diploid, bisporangial phase; and the presence of a prominent stalk cell subtending the tetra/bisporangium. Silva & Johansen (1986) make no firm proposal as to where the Corallinales belongs in the red algal hierarchy, although they consider it to be a highly specialized order which 'might well be placed just before the Ceramiales'. Other possibilities are suggested in a cladistic analysis by Gabrielson & Garbary (1986). Woelkerling (1988: 84) discusses Silva & Johansen's concept of the Corallinales and points out that many of the characters are shared with other red algal orders. He also shows that not all the characters are present in all coralline algae.

Silva & Johansen (1986) and Woelkerling (1988) suggest that the time is not yet ripe to raise all the currently accepted subfamilies to family status; I have, therefore, retained the single family, Corallinaceae, with the subfamily Lithophylloideae to which *Titanoderma* belongs.

The Lithophylloideae is characterized by the presence of single-pored, tetra/bisporangial conceptacles and secondary pit connections between cells of contiguous thallus filaments, cell fusions occur very rarely. At present two circumscriptions of the subfamily are in use. Johansen (1969, 1976*a*, 1981), Adey & Johansen (1972), Adey & MacIntyre (1973), and Woelkerling (1987, 1988) restrict the Lithophylloideae to nongeniculate genera and segregate geniculate genera in the Amphiroideae. Cabioch (1971*a*, 1972, 1988), on the other hand, includes both geniculate and nongeniculate genera in the Lithophylloideae sensu lato. The close relationship between the geniculate and nongeniculate genera concerned is not, however, in dispute and I have used the Johansen scheme (Chamberlain, 1983: 331) as a 'taxonomically functional classification' while recognizing that Cabioch's scheme represents a more acceptable evolutionary hypothesis (Chamberlain, 1978*b*, 1983).

With the exception of the parasitic genus *Ezo* Adey, Masaki & Akioka (1974), most smaller members of the Lithophylloideae are found in *Titanoderma*. Some *Titanoderma* species have a bistratose vegetative thallus composed of axial and epithallial cells only, but most species develop erect filaments varying with the species to about 20 (exceptionally 80–90) cells long. Cells of axial and erect filaments are usually vertically elongated and axial cells are characteristically orientated at an oblique angle to the substratum in radial VS (Figs 9–11), a configuration known as palisade. Cabioch (1972, 1988) regards the genus as the simplest member of a lithophylloid series that also includes *Tenarea*, *Goniolithon*, and the geniculate genera *Amphiroa* and *Lithothrix*. A second lithophylloid series, including the type genus *Lithophyllum*, comprises genera which, like *Titanoderma*, have a unistratose, basal layer of filaments but with cells that are more nearly isodiametric in radial VS, and vertically rather than obliquely orientated. Cabioch (1972, 1988)



Figs 24–29 Scanning electron micrographs to show thallus features of *Titanoderma* (scales in μm).

24. Edge (arrow) of thallus surface of *T. pustulatum* var. *pustulatum* (86/147) showing axial filaments (a) and epithallial concavities (e).
25. Lower surface of var. *pustulatum* (84/150) showing radiating axial filaments (a) and down-curved edge. Pseudodichotomous branching (arrow) occurs in the filaments
26. Detail of Fig.25 showing down-curved calcification (c) protecting the axial filament initials (i).
27. Surface of central area of thallus of the type specimen of *T. pustulatum* var. *pustulatum* showing honeycomb-like calcified ridges surrounding epithallial concavities (e). Sometimes the calcification splits at the middle lamella (arrow).
28. Surface of Børgesen's specimen (C) of *Lithophyllum hapalidioides* (= *T. pustulatum* var. *pustulatum*) from the Faeröes showing calcified ridges surrounding epithallial concavities (left) and superimposed calcareous deposition (right) with lines demarcating areas of deposition (arrow).
29. Surface of *T. pustulatum* var. *confine* (79/208) showing a trichocyte (arrow).

recognizes a more primitive genus, *Pseudolithophyllum* Lemoine (1913*a*) and a more advanced genus *Lithophyllum* in this second series, together with the parasitic genus *Ezo*. The distinction between *Lithophyllum* and *Pseudolithophyllum* is based on the occurrence of secondary growth of the erect component to produce an extensive area of filaments ('faux hypothalle') in *Lithophyllum* but not in *Pseudolithophyllum*. A concise analysis of the current situation regarding the classification of the Lithophylloideae is presented in Johansen (1981: 41–44).

While the present text was in press, the genus *Titanoderma* was subsumed in *Lithophyllum* by Campbell & Woelkerling (1990). The authors based this action on the assumption that the only character separating the genera was the predominance of tall, oblique, palisade cells in the axial filaments of *Titanoderma*, as opposed to relatively short, vertically orientated ones in *Lithophyllum*. Such a distinction has been accepted by Cabioch (1972, 1988), Johansen (1981), Woelkerling et al. (1985), and Woelkerling (1988) among others. Campbell & Woelkerling (1990) pointed out that palisade cells sometimes occur in *Lithophyllum* and short, straight ones in *Titanoderma*, thus invalidating the generic distinction.

In the course of investigating the British Isles coralline flora (in preparation), Linda Irvine and I examined these two genera and concluded that, while the **predominance** of palisade and squarish axial cells in *Titanoderma* and *Lithophyllum* respectively, **might** suffice as a diagnostic character to maintain two genera, a further diagnostic character separated them decisively. We noted (Chamberlain et al., 1991) that all species of *Titanoderma* showed at least some bistratose thallus (comprising axial and epithallial cells only) at the margin and/or in regenerating thallus areas. In *Lithophyllum*, in contrast, no bistratose thallus occurs either marginally or in regenerating thallus. This characteristic is confirmed in the respective generitype specimens: *Titanoderma pustulatum* (Woelkerling et al., 1985, figs 30–32) and *Lithophyllum incrustans* (Woelkerling, 1983, figs 18–19). We have found no species that have predominantly palisade axial cells but entirely lack bistratose thallus, nor species with predominantly squarish axial cells that have any bistratose thallus. We note, however, that some species of *Titanoderma* such as *T. corallinae* (q.v.) may have thalli that thicken immediately behind the marginal initial, like *Lithophyllum*, **in addition** to bistratose areas.

TITANODERMA: Basic features

Spore segmentation

Spore segmentation in *Titanoderma* is of the *Dumontia*-type (Chemin, 1937) in which spore segmentation produces up to 32 cells within the confines of the original spore wall before further development occurs. This pattern occurs in all investigated species of Corallinaceae with the exception of parasitic species such as *Choreonema thuretii* (Bornet) Schmitz (Cabioch, 1971*b*).

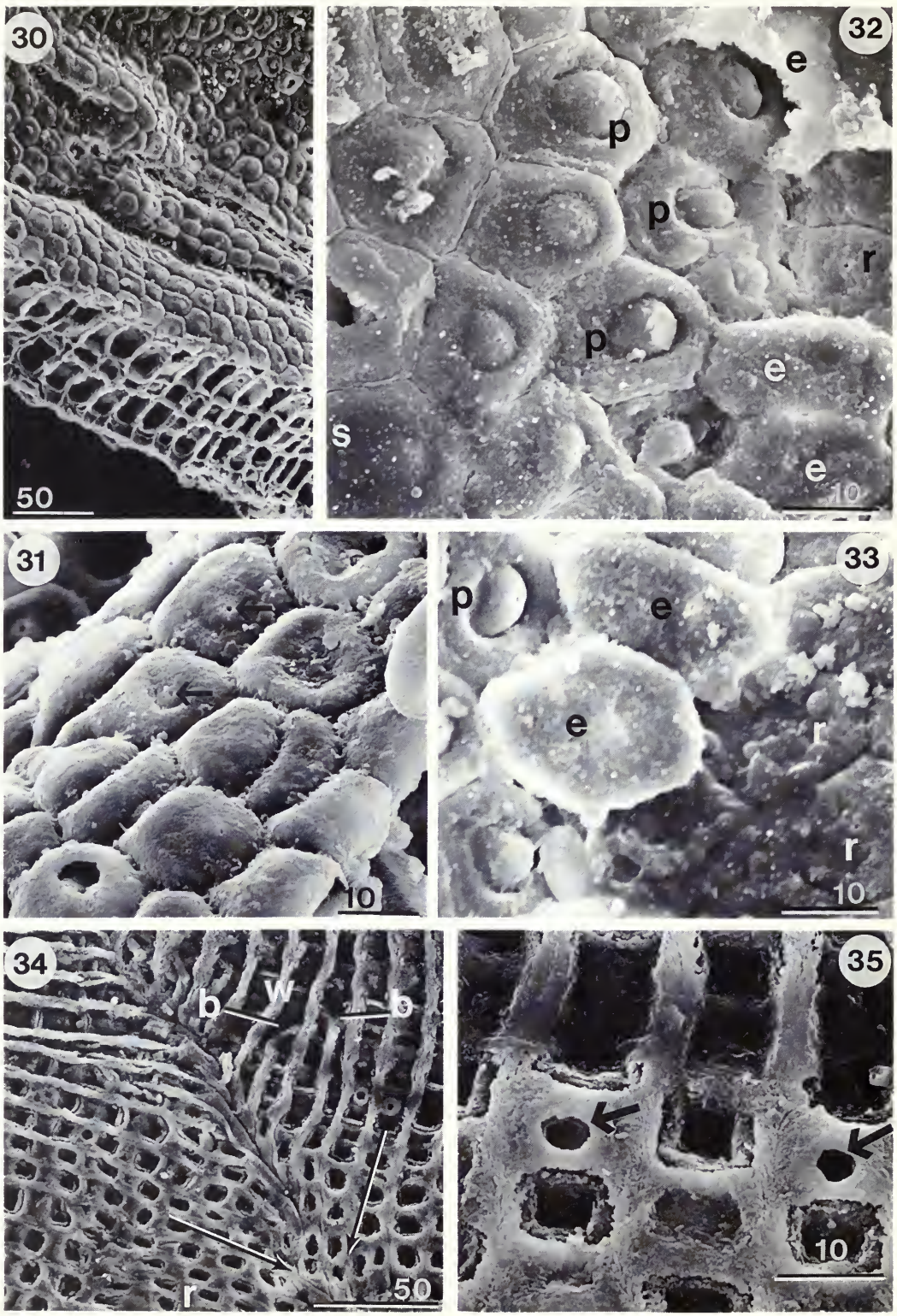
Spore segmentation patterns in the Corallinaceae were studied by Chihara (1972, 1973, 1974*a*, 1974*b*), Notoya (1974, 1976*a*, 1976*b*), Bressan (1980), Chamberlain (1983, 1984), and Jones & Woelkerling (1984) who all recognized that particular sequences could be related to taxonomic groupings. Chihara (1972, 1973) recognized a pattern in the geniculate genera *Lithothrix* and *Amphiroa* which he subsequently (Chihara, 1974*a*, 1974*b*) demonstrated in *Titanoderma* (as *Dermatolithon*) and *Lithophyllum* belonging to the Lithophylloideae, calling this the *Amphiroa*-type. Notoya (1974) confirmed this pattern in three species of *Titanoderma* (as *Tenarea*), the developmental stages of which are illustrated diagrammatically in Fig. 1. A *T. corallinae* sporeling under SEM is shown in Fig. 3, and a sporeling of *T. pustulatum* var. *pustulatum* is seen in Figs 2 and 4.

Cabioch (1972) studied the further development of sporelings and showed that, in what she termed the *Lithophyllum*-mode, a single layer of marginal initials is cut off peripherally by simple divisions of the radiating (axial) filaments (Cabioch, 1972, fig. 9) and that epithallial cells, secondary pit connections, and, not infrequently, trichocytes arise early in sporeling development.

Thallus structure and morphogenesis

Continuation of the *Lithophyllum*-mode of development (Fig. 2) results in a single, basal layer of radiating axial filaments that are produced by division of terminal initials. After formation, each axial cell cuts off an epithallial cell on its upper, distal edge that is generally more or less ovate to orbicular in surface view (Fig. 15a) and triangular in radial VS (Figs 9–13). In radial VS, cells of axial filaments are characteristically tall, obliquely orientated, and often sinuate (Figs 9–11): they are alternatively known as palisade cells (Woelkerling, 1988: 16). Successive axial cells are joined by primary pit connections which usually occur in the top third of the cells (Fig. 9). Secondary pit connections may develop close to primary ones (Fig. 9), or between cells of contiguous filaments. Increase in circumference of the thallus is accomplished by pseudodichotomous divisions in the axial filaments in the horizontal plane (see Figs 25, 34). In some taxa (e.g *T. pustulatum* var. *canellatum*) vegetative growth is entirely bistratose, being confined to axial filaments and epithallial cells, and further development occurs only in relation to conceptacle production. Other species (e.g. *T. prototypum* (Foslie) Woelkerling, Y. Chamberlain & P. Silva and *T. tessellatum* (Lemoine) Woelkerling, Y. Chamberlain & P. Silva) likewise do not produce erect filaments, but successive, superimposing axial layers develop; the appearance of these thalli in VS, with alternating 'layers' each composed of axial and epithallial cells (Figs 5, 6), is similar to that seen in the mastophoroid genus *Lithoporella* (cf. Lemoine, 1974). Turner & Woelkerling (1982*a*) showed that this thallus form results from branching of a single plant and not from the superimposition of many separate individuals as previously supposed; it is probable that the same situation occurs in *Titanoderma* but this has not yet been substantiated.

In most species of *Titanoderma* erect filaments develop which vary in length depending on the species, but in relatively few species do they exceed about 20 cells (cf. Lemoine, 1971). An erect filament originates from an axial cell which divides longitudinally (Figs 10, 11) to produce an upper and lower cell, or occasionally two upper cells (Fig. 12). The upper cell(s), which now bears the epithallial cell, remains meristematic and in thicker species it continues cutting off cells (Fig. 11) from its lower surface in a manner seen in other corallines such as *Fosliella* and *Pneophyllum* (cf. Chamberlain, 1983: 320). Sometimes the subepithallial initial divides pseudodichotomously (Fig. 13). The subepithallial initial is,



Figs 30–35 Scanning electron micrographs to show features of thallus surface cells in *Titanoderma* (scales in μm).

30. VS and surface view of *T. pustulatum* var. *macrocarpum* (86/159c).

31. Detail of surface seen in 30. The flat topped epithallial cells have a slightly raised surface with small central hole (arrow) marking the pit connection with the previously shed epithallial cell.

32 & 33. Surface view of var. *macrocarpum* (Adey 70–6–B) showing the roofs of epithallial cells (r) on the thallus surface. The epithallial cells (e) are then shed revealing a newly protuberant epithallial cell (p) below which gradually flattens to form the new thallus surface.

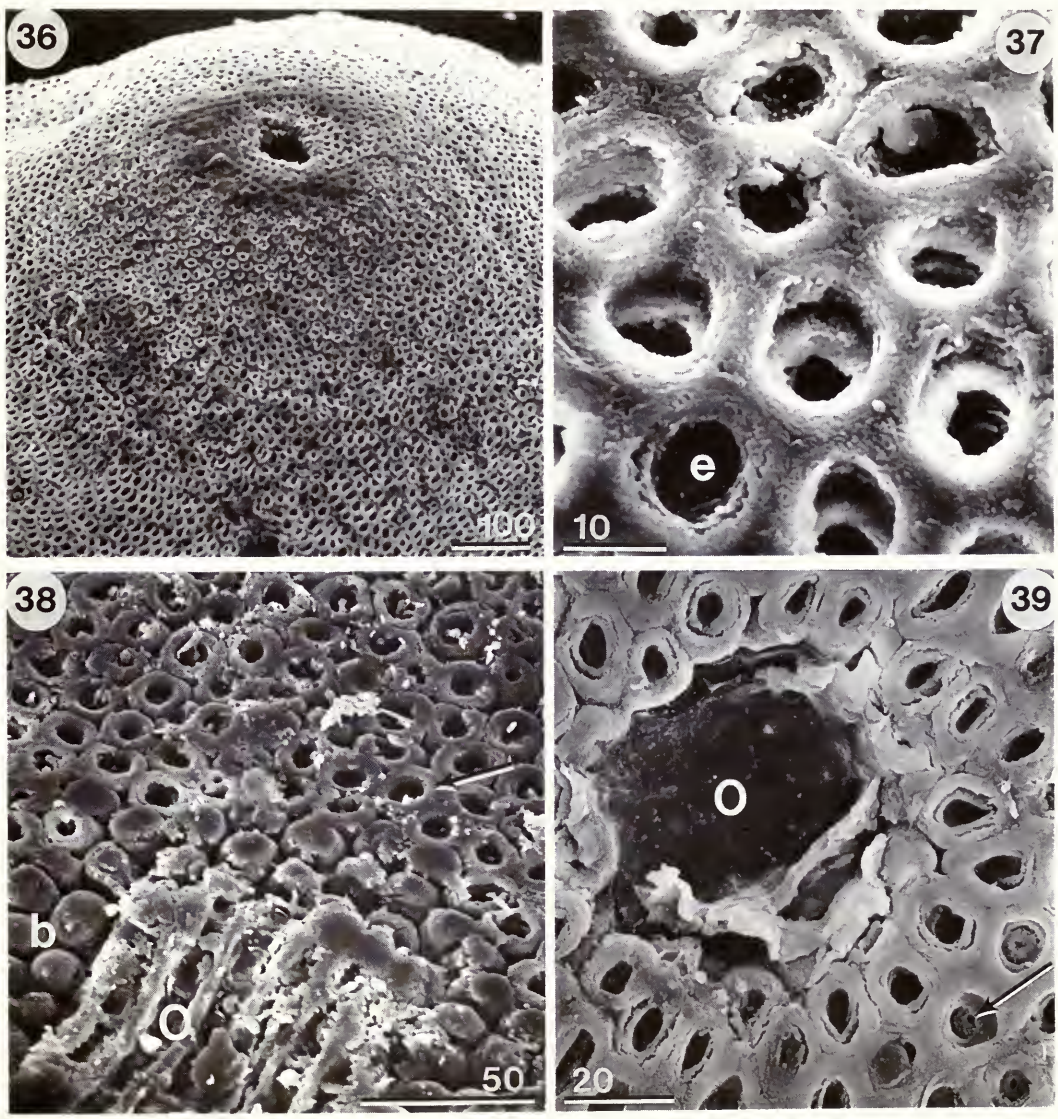
34. Surface view of two contiguous var. *pustulatum* thalli (84/147) at an early stage of calcification. The side walls (w) of some axial cells have calcified before the roofs (r). Pseudodichtomous branching is evident in some filaments (b), direction of growth indicated by arrows.

35. Detail of thallus in Fig.34 showing two trichocytes (arrows).

therefore, intercalary and subapical, which is regarded as a taxonomically distinguishing feature of the Corallinales (Silva & Johansen, 1986).

Cells of erect filaments, like axial cells, tend to be vertically elongated in VS (e.g. Fig. 14) and, in this case, may be termed columnar cells (Woelkerling, 1988: 16). Contiguous cells usually occur in rather regular, if often sinuate, horizontal 'rows' and are often joined by secondary pit connections (Fig. 11). A common feature of many species of *Titanoderma* is a tendency to regenerate axial filaments from thallus cells that have become damaged or obstructed (Fig. 14). Cabioch (1972: 193–194) described and figured this characteristic regeneration.

As a result of her morphogenetic studies, Cabioch (1972: 194) concluded that *Titanoderma* differs from other coralline genera in that when a hypothallial (axial) cell divides to produce the first perithallial (erect filament) cell, the primary pit connection is generally continued in that cell (Cabioch, 1972, fig. 12D), rather than in the hypothallial cell (Cabioch, 1972, fig. 12C) as is usual in other genera. The implication is that the subepithallial cells of such thalli become homologous with hypothallial cells which then continue to cut off cells downwards. To be pragmatic she concluded that the term hypothallium should continue to be applied to the basal cell layer, while keeping in mind the peculiarity of its origin. I have examined this feature particularly in the type species *T.*



Figs 36–39 Scanning electron micrographs to show conceptacle roof features in *Titanoderma* (scales in μm).

36. Mature conceptacle of *T. pustulatum* var. *pustulatum* (84/146) showing that there is no abrupt differentiation between conceptacle roof and thallus surface.

37. Surface of conceptacle roof seen in Fig. 36 with calcified cell walls encircling epithallial concavities (e).

38. Surface of roof of young var. *pustulatum* conceptacle (81/1); the ostiole (o) is covered with remnants of old thallus cells. Bulbous epithallial roofs (b) occur on cells immediately surrounding the ostiole but these collapse in older cells as the surrounding cell walls (arrow) become calcified and encircle the epithallial concavities.

39. Conceptacle of var. *pustulatum* (86/147) slightly more mature than Fig.38. The ostiole (o) is surrounded by heavily calcified cells. In some concavities the epithallial cells have disintegrated revealing the pit connection with the subtending cell (arrow).

pustulatum (Figs 9, 10), but in all sections, detailed examination showed that the primary pit connection apparently continued in the axial filament although first appearances were sometimes deceptive. It would seem that further, specific data are required to evaluate Cabioch's hypothesis.

As has been discussed, the epithallial cell, which is often triangular in radial VS, remains on the surface of the subepithallial initial (Figs 9–11); in *Titanoderma* it is rare for tiers of epithallial cells to occur but, in actively growing plants at least, new epithallial cells are probably being continually produced from the outer surface of the initial as old epithallial cells are sloughed off (Fig. 10, see also pp. 46, 55). Various authors (e.g. Giraud & Cabioch, 1976, 1977; Bressan, Ghirardelli & Bellemo, 1981) have shown that the coralline epithallial cell is the seat of very active physiological processes and continual renewal of these mainly uncalcified cells is presumably essential for the physiological maintenance of the plant. The epithallial cell is calcified only lightly, if at all, on the outer surface but as can be seen in SEMs (e.g. Fig. 27), it is cupped below in the calcified upper wall of the initial.

The cytological features of cells of axial and erect filaments of *Titanoderma* are very similar; in many species their cytoplasmic contents are very sparse and are principally located at the tops of the cells, particularly in the vicinity of pit connections, although sometimes the contents are denser and more evenly distributed. Starch grains (Figs 6, 8) in various stages of development (cf. Cabioch, 1971*b*: 138 et seq.) have been observed in most species, principally in lower parts of the thallus. The amount of starch varies both within and among species: in epiphytic plants of *T. pustulatum* var. *pustulatum* for example, starch is often absent, but large starch grains are particularly prevalent in var. *macrocarpum* (Figs 102, 104). Cell wall calcification is not usually very heavy and the shape of the cell lumen is mainly more or less rectangular in VS (Fig. 7), although the heavy calcification seen in species of *Lithophyllum* such as *L. crouanii* (Foslie) Foslie (see Chamberlain et al. 1988), occurs to a lesser degree in var. *macrocarpum* (Fig. 8). In British Isles taxa secondary pit connections in *Titanoderma* characteristically occur in the upper third of the cell (e.g. Fig. 11) as compared with *Lithophyllum* in which they are mainly half way down the cell or lower.

Trichocytes have been observed in cells of axial and erect filaments in *T. pustulatum* var. *confine* (e.g. Suneson, 1943: 37 as *Lithophyllum litorale*; Chamberlain, 1978*a*, fig. 2, as *Dermatolithon litorale*), and rarely in other taxa but they occur much less frequently than in mastophoroid algae such as *Fosliella* and *Pneophyllum* (Chamberlain, 1983). They are simple structures comprising a small cell attached to the side of subepithallial initials (Fig. 15); it is easy to miss seeing them in section but they are often apparent in thalli and conceptacles seen under SEM (e.g. Figs 29, 35).

Cabioch (1972: 175; 1988) considers what she terms simple, nongeniculate crustose corallines like *Titanoderma* to be neotenic, being derived from more complex, slow growing forms by a process of rapid development and early reproduction. This is a possible concept with respect to the thin species of *Titanoderma*, but massive species also occur within the genus and these could not be interpreted in this way.

Reproduction

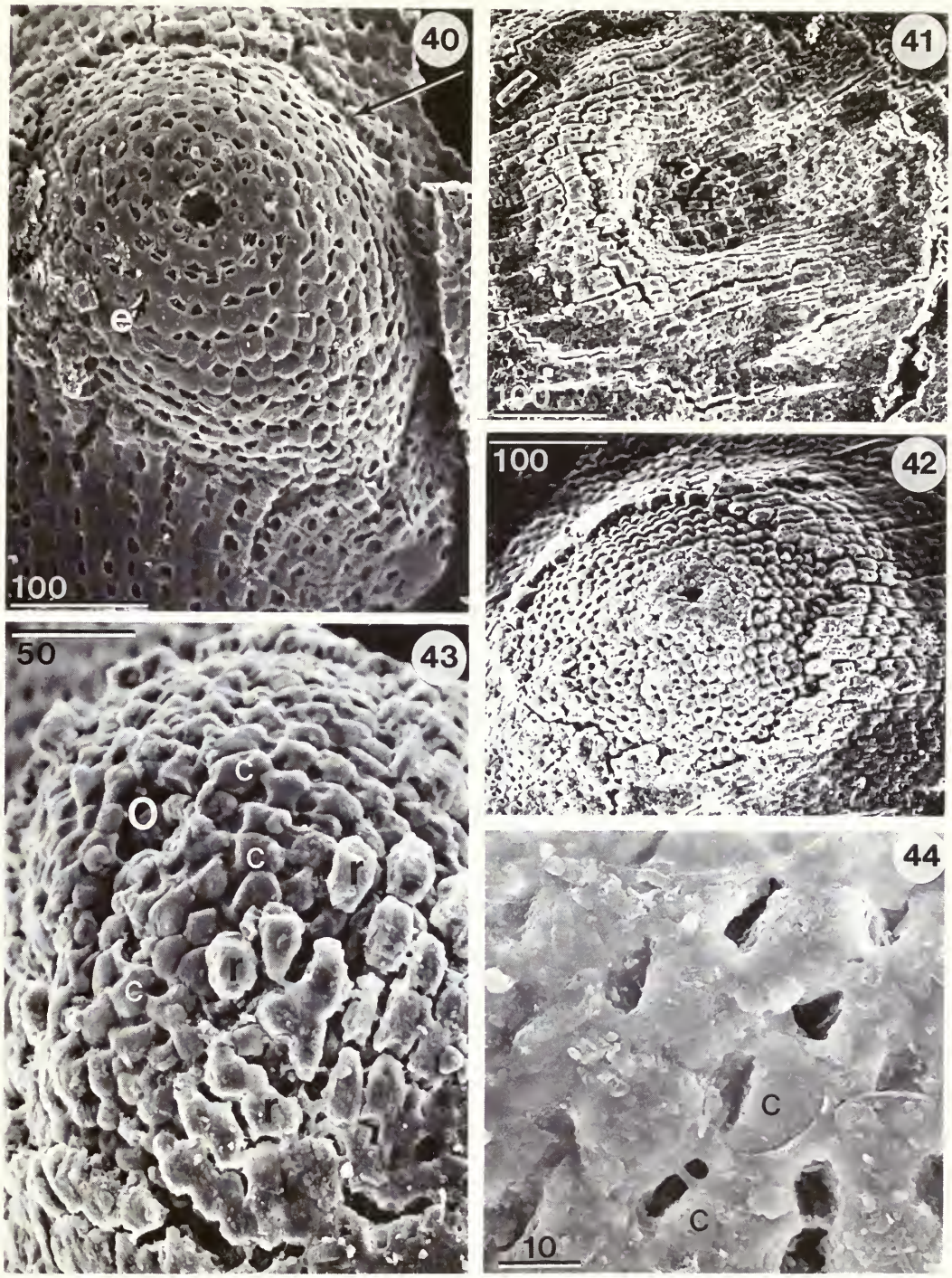
Spermatangial plants

Gametangial plants may be monoecious or dioecious even within the same species; spermatangial conceptacles usually have relatively broad, shallow chambers that are more or less triangular in VS (Fig. 16). Spermatangial initials originate in a circular disc-like conceptacle primordium in the subepithallial initials; this disc develops into the conceptacle floor as surrounding filaments overgrow it to form the roof (Fig. 16). Johansen (1976*a*: 235, fig. 63, table 2) designated this type of conceptacle development as 'sur'-roof, formed by overgrowth of filaments surrounding fertile areas. Spermatangial initials cut off spermatangia, usually from at least two loci (Fig. 16), the spermatangia are elongate when attached but round off when released into the conceptacle chamber. Spermatangia are released through the single ostiole, which is often prolonged into a spout (e.g. Fig. 246). The structure and development of spermatangial conceptacles in plants that would now be classified in *Titanoderma* was described and illustrated in detail by Suneson (1943, in *Lithophyllum corallinae*), Tokida & Masaki (1959, in *Dermatolithon tumidulum*), and Masaki & Tokida (1960*a*, in *D. corallinae* and 1960*b*, in *D. dispar* and *D. canescens*). Their relatively simple structure, with elongate spermatangia arising from unbranched initials carried only on the conceptacle floor and not the roof, is seen throughout the Lithophylloideae and Mastophoroideae (Lebednik, 1978).

Carpogonial/carposporangial plants

The structure and development of carpogonial/carposporangial conceptacles in *Titanoderma* was described and illustrated by Suneson (1943, in *Lithophyllum corallinae*), Tokida & Masaki (1959, in *Dermatolithon tumidulum*), and Masaki & Tokida (1960*a*, in *D. corallinae* and 1960*b*, in *D. dispar* and *D. canescens*). As with the spermatangial conceptacle, carpogonia originate in a primordial disc of subepithallial initials and growth of surrounding erect filaments occurs to form the conceptacle roof and ostiole canal (Fig. 17). Central carpogonial branches are fertile and each produces a single carpogonium prolonged into a trichogyne; there may be a sterile lateral cell (Fig. 17). Peripheral carpogonial branches remain sterile (Fig. 17), as generally occurs in corallines (Lebednik, 1978). After presumed fertilization, a continuous fusion cell (see Lebednik, 1977: 384) develops on the conceptacle floor. Gonimoblast filaments arise from either the extreme periphery (Fig. 18), or the lower surface of the periphery (Fig. 244), of the fusion cell. Lebednik (1977: 385) showed that peripheral gonimoblast development pertains throughout the nongeniculate Lithophylloideae. In many species of *Titanoderma* and *Lithophyllum* (see Masaki, 1968) the sterile, outer carpogonial branches on the surface of the fusion cell swell and become conspicuously clavate (Figs 18, 238) as the carposporophyte develops. This swelling is common within the Lithophylloideae and is possibly concerned with the nutrition of the fertile cells.

Mature carposporangial conceptacles may be raised above or immersed within the thallus. They usually have small, slightly papillate cells surrounding the ostiole and occasionally these are more conspicuously developed, but no elaborate ostiole filaments like those seen in *Pneophyllum* (Chamberlain, 1983) have been observed. Gonimoblast filaments continue to develop and the terminal carposporangium is released through the ostiole. In general, the features of *Titanoderma* conceptacle structure and development are very similar to those of known species of *Lithophyllum* and confirm the close taxonomic relationship between the genera.



Figs 40–44 Scanning electron micrographs to show conceptacle features in *Titanoderma* (scales in μm).

40. Conceptacle of the type specimen of *Melobesia verrucata* (= *T. pustulatum* var. *canellatum*) (CN) showing the step-like cells of the conceptacle roof with heavily calcified cells subtending epithallial concavities (e). The thallus forms a 'skirt' at the conceptacle base (arrow).

41 & 42. Developing conceptacles of *T. pustulatum* var. *confine* (minute growth form) (76/279). In Fig. 41 the conceptacle remains beneath the thallus surface which is starting to disintegrate. In Fig. 42 the conceptacle has ruptured the thallus surface and step-like roof cells are already well formed.

43. Young conceptacle of var. *confine* (minute growth form) (79/208). The ostiole (o) is surrounded by developing roof cells (c) and remnants of the old thallus surface (r) remain in places.

44. Surface of an old roof of var. *confine* (minute growth form) (80/9) in which the step-like calcification has become flattened (c).

Tetra/bisporangial plants

The tetra/bisporangial conceptacle of *Titanoderma* has a single, apical pore through which its sporangia are released. In most species the conceptacle is a raised, domed structure (e.g. Fig. 36), but in some species with thicker thalli (e.g. *T. corallinae, T. laminariae)* conceptacle chambers may be completely immersed in the thallus with the roof flush with the thallus surface (Fig. 229).

The development of the bisporangial conceptacle of the generitype *T. pustulatum* proceeds as follows:

(1). A disc of epithallial cells (Fig. 19) starts to slough off. Below these cells a primordial ring of subepithallial initials becomes more densely pigmented than surrounding cells and each divides into a lower stalk cell and upper sporangial initial.

(2). Thallus cells surrounding the sporangial initials become stretched and begin to rupture (Fig. 20), the uppermost cells remain to form the conceptacle roof and a central group of filaments persists as a columella.

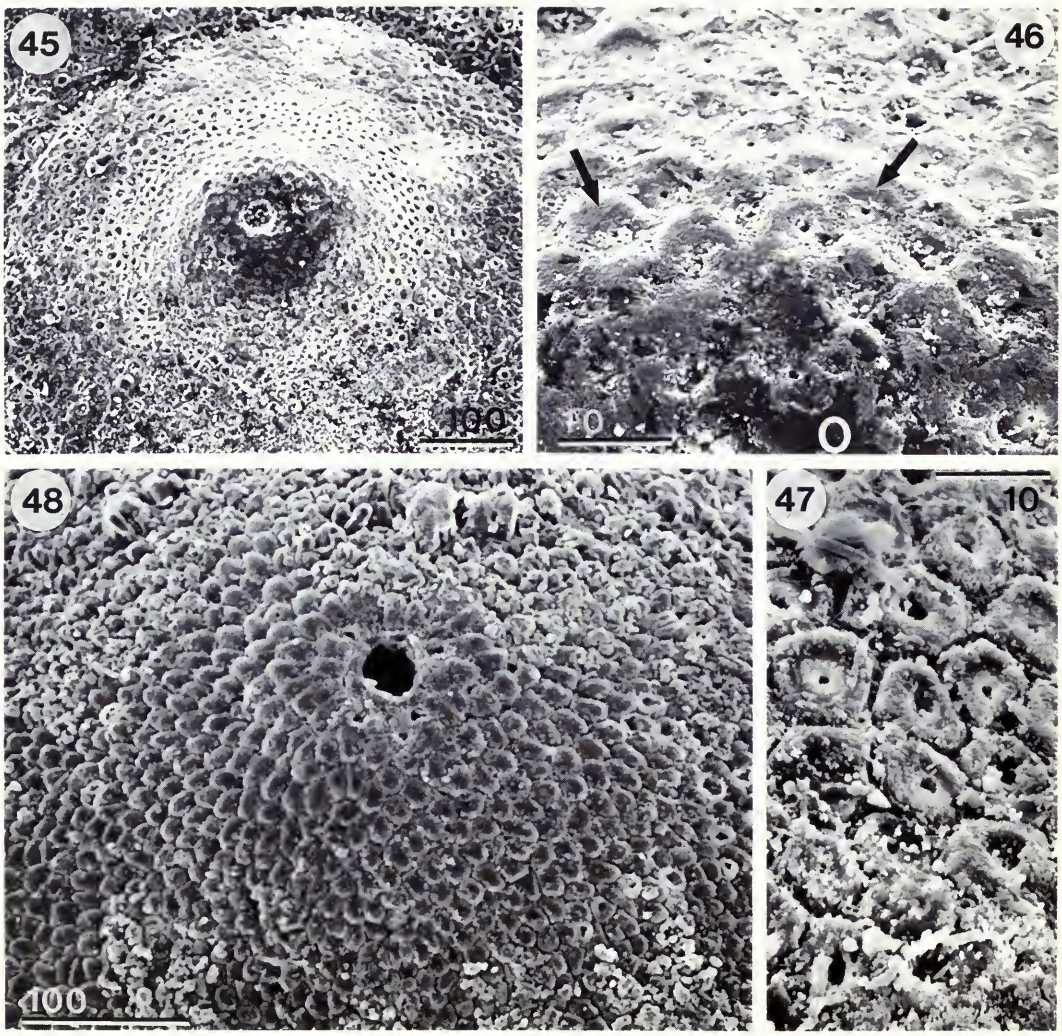
(3). The roof cells enlarge and the roof becomes arched (Fig. 21). The cells of the columella filaments enlarge.

(4). The tops of the columella cells rupture (Fig. 22), creating a central roof ostiole and leaving wispy remnants below, in the centre of the conceptacle. The sporangial initials start to enlarge.

(5). Sporangia enlarge further and divide (Fig. 23), they are then released through the ostiole. The empty conceptacle usually becomes filled in, but in *T. laminariae, T. pustulatum* var. *macrocarpum,* var. *confine*, and some forms of var. *pustulatum*, old conceptacle chambers may become immersed in the thallus (e.g. Fig. 66).

The entire contents of the conceptacle appear to be somewhat mucilaginous in the middle stages of development. Possibly this ensures retention of immature sporangia even if the ostiole is already open.

This type of development has been described and figured in tetra/bisporangial conceptacles by such authors as Nichols (1909, pl. 12), Suneson (1943), Tokida & Masaki (1959, in



Figs 45–48 Scanning electron micrographs to show conceptacle roof features in *Titanoderma* (scales in μm).

45. The cone-like mature conceptacle of the lectotype specimen of *Melobesia hapalidioides* (= *T. pustulatum* var. *macrocarpum*) (CO)
46. The cells below the ostiole (o) in Fig. 45 have horseshoe-shaped calcification (arrow) below a small hole.
47. The roof cells in Fig. 45 gradually transmute towards the cells at the conceptacle base which have raised cell surfaces with a central hole presumably due to epithallial shedding.
48. Young conceptacle of var. *macrocarpum* (84/229) showing the cone-like roof with bulbous cells.

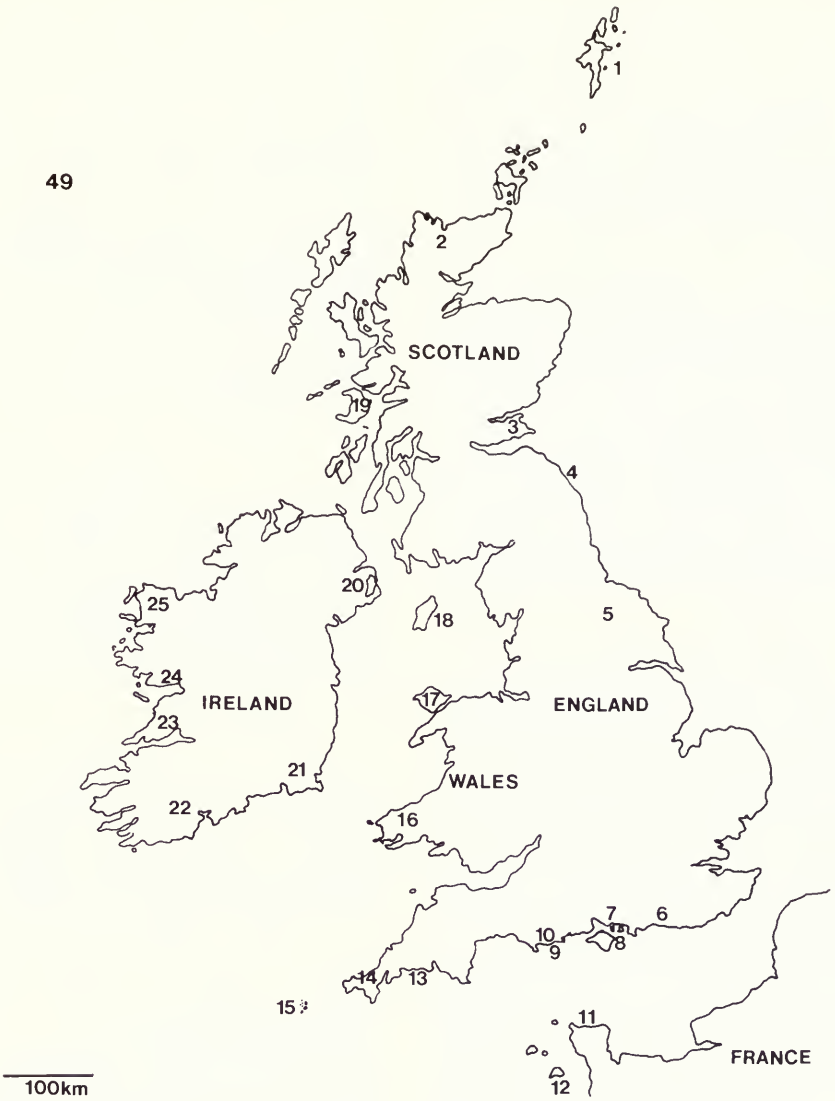


Fig 49 Map of the British Isles and northwestern France to show principal collecting localities for *Titanoderma*.
1 = Shetland Is, 2 = Sutherland, 3 = Fife, 4 = Berwick-upon-Tweed, Northumberland, 5 = Yorkshire, 6 = Sussex, 7 = Hampshire, 8 = Bembridge, Isle of Wight, 9 = Kimmeridge, Dorset, 10 = Lulworth, Dorset, 11 = Cherbourg, 12 = Jersey, 13 = Wembury, Devon, 14 = Cornwall, 15 = Isles of Scilly, 16 = Dyfed, 17 = Anglesey, 18 = Isle of Man, 19 = Isle of Mull, 20 = Co. Down, 21 = Co. Wexford, 22 = Co. Cork, 23 = Co. Clare, 24 = Co. Galway, 25 = Co. Mayo.

Dermatolithon tumidulum), and Masaki & Tokida (1960*a*, in *D. corallinae* and 1960*b*, in *D. dispar* and *D. canescens*). Tetrasporangial conceptacles differ from bisporangial ones only in that tetrasporangial initials divide simultaneously and zonately into four spores, a feature regarded as a significant taxonomic characteristic of the Corallinales (Guiry, 1978*a*; Silva & Johansen, 1986).

Johansen (1976*a*, 1981) incorporated this type of tetra/bisporangial conceptacle roof development into a tabular key, designating it as 'col', i.e. 'roof formed by growth of filaments interspersed among the sporangia as well as by centrally located tuft of sterile filaments called a columella; pore formed by breakdown of upper part of columella' (Johansen, 1976*a*: 235, fig. 60). This type of development was found by Johansen to occur in all genera of the Lithophylloideae and this general conclusion was upheld in a survey by Townsend (1981).

It is probable that bisporangial plants and uninucleate bispores are diploid in *Titanoderma*; Suneson (1950) established cytologically that meiosis did not occur in the production of uninucleate bispores in *T. pustulatum* var. *confine* and *T. corallinae* (as *Lithophyllum litorale* and *L. corallinae* respectively) whereas it did occur in the production of binucleate bispores in *T. corallinae*. Later Suneson (1982) demonstrated, in cultured plants, that bispores gave rise to further bisporangial plants in var. *confine* (as *Dermatolithon litorale*). No further life history sequences have been completed in cultured *Titanoderma* plants, but it seems likely that both a *Polysiphonia*-type, and a self-perpetuating bisporangial-type life history are present in the genus, as has been demonstrated in *Fosliella* and *Pneophyllum* (Chamberlain, 1983, 1987).

Bisporangial plants are predominant in northern European populations of *Titanoderma* (cf. Suneson, 1943; Hamel &

Lemoine, 1953; Chamberlain, 1978*b*), but in warmer localities such as the Canary Islands (unpublished observations), California (Nichols, 1909), Pacific Mexico (Dawson, 1960), and India (Ganesan, 1962), and also in Japan (Masaki, 1968), gametangial/tetrasporangial plants are the norm and bisporangial plants rare or absent. It appears, therefore, that apomictic bisporangial reproduction is an adaptation to the climate in the colder parts of the distribution range of *Titanoderma*, as postulated by Suneson (1950).

Ecology

Titanoderma is most frequently observed as an epiphyte on other species of marine algae and seagrasses. It also occurs quite commonly as a lithophyte or epizoically on limpets and other marine animals. The genus is not normally a conspicuous shore feature in temperate waters although a species with a thick thallus, *Dermatolithon nodulosum* Y. Chamberlain, is a conspicuous feature of intertidal pools on Gough Island, south Atlantic (Chamberlain, 1965; Chamberlain, Holdgate & Wace, 1985). Another species, *T. prototypum*, plays an important role in binding loose substrata on tropical coral reefs (D. Littler et al., 1989: 218).

TITANODERMA—TAXONOMY OF BRITISH ISLES PLANTS

Introduction

Considerable difficulty has been found in characterizing and identifying taxa of *Titanoderma*, which has, in many ways, been more pronounced than with *Fosliella* and *Pneophyllum* (Chamberlain, 1983) where such characters as conspicuous ostiole filaments often proved diagnostic and facilitated identification. This problem may stem from the fact that most *Titanoderma* plants in the British Isles are bisporangial and therefore, presumably, apomictic. However, recently examined material (unpublished) from northern Spain, the Mediterranean, and the Canary Islands suggests that the taxa now proposed will be largely confirmed when gametangial/tetrasporangial populations are more widely available.

On the basis of the presence of either immersed or raised tetra/bisporangial conceptacles, *Titanoderma* in the British Isles can be divided into two groups:

T. laminariae and *T. corallinae* with immersed conceptacles

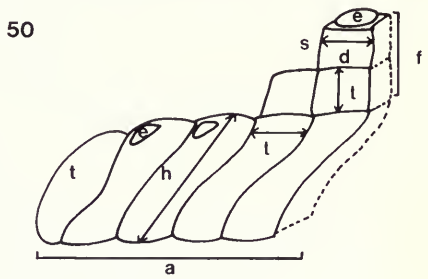
T. pustulatum with raised conceptacles.

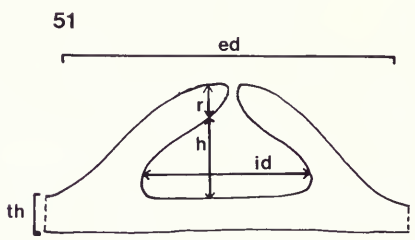
The first two species are differentiated principally on conceptacle size. Within *T. pustulatum* however, there is a very wide and continuous matrix of variation with four focal points now designated as varieties. To quote Davis & Heywood (1963: 75) 'no single diagnostic character may distinguish the [varieties], they can only be separated by a combination of differential characters any one of which may break down individually'. Possible differential characters for all the above taxa are now explored:

Dimensions

Throughout his publications, Foslie used dimensions as diagnostic characters and this practice has persisted throughout coralline work. Adey & Adey (1973) give minimum, mean and maximum values for all dimensions they quote, and I have found this useful in practice, even when based on small samples. Nowadays, however, extensive statistical analysis is required to support 'mean' values and for the most part authors quote only minima and maxima, sometimes with extreme values in brackets. Such values tend to be similar across the taxa under investigation which may mask generally perceived differences such as the relatively small conceptacles of *T. corallinae* and *T. pustulatum* var. *canellatum*. Nevertheless, for the most part I have adopted the minimum/maximum practice, but standard deviations have been calculated with respect to certain characters in the *T. pustulatum* complex (Table 1, p. 23).

Dimensions are measured as shown in Figs 50 and 51.





Figs 50–51 Diagrammatic vertical sections of *Titanoderma* to indicate dimensions measured.

50. Vegetative thallus.

51. Tetra/bisporangial conceptacle.

a = axial filament, d = diameter, e = epithallial cell, ed = external diameter, f = erect filament, h = height, id = internal diameter, l = length, r = roof thickness, s = subepithallial initial, t = terminal initial, th = thallus thickness.

Colour

As observed by Adey & Adey (1973: 371, 372), absolute colour is a very variable character in coralline algae. Nevertheless relative colour values can be a useful guide to identity: Adey & Adey found, for example, that in any one mixed sample, thalli of *Phymatolithon lenormandii* (Aresch. in J. Agardh) Adey are always bluer than those of *P. laevigatum* (Foslie) Foslie. This is also true for *Titanoderma* in the British Isles: the blueish/violet colour of *T. pustulatum* var. *confine*, for example, may be very striking and this perception has persisted from the original description (Crouan & Crouan, 1867) to recent observations (Hamel & Lemoine, 1953; Adey & Adey, 1973). I have based colour values on freshly collected material and neither herbarium specimens nor liquid preserved plants can be used reliably for this purpose. Colour values are related, as far as possible, to shades in the *Methuen handbook of colour* (Kornerup & Wanscher, 1978). In common with colleagues, I find that while an overall perception of colour may relate to one shade in the book, a fragment

of plant placed beside a colour block may match a different shade. The Methuen colours quoted, therefore, refer to detailed matching while the general impression is conveyed in more general terms such as blueish, reddish, mauve-pink, etc.

Thallus characters

Margin

All varieties of *T. pustulatum* have a more or less extensive bistratose margin in which only axial and epithallial cells are present (e.g. Figs 9, 106). The thalli of *T. corallinae* and *T. laminariae* (e.g. Fig. 229), by contrast, often thicken immediately behind the terminal initial giving their thalli a chunky look. A bistratose margin may, however, develop in rapidly growing plants and/or areas of regeneration.

Imbrication

Thalli of *T. corallinae, T. laminariae, T. pustulatum* var. *pustulatum* and var. *canellatum* usually have an entire, flat surface; in *T. pustulatum* var. *macrocarpum* (Fig. 142) and var. *confine* (Fig. 14), however, thallus regeneration often occurs to form imbricating lobes. In one growth form of var. *macrocarpum* the vegetative thallus consists almost entirely of imbricating lobes composed of axial filaments (Figs 151, 154).

Axial filaments

Palisade cells of axial filaments are usually tall, obliquely orientated, and often sinuate (e.g. Figs 9, 101, 199), but squarish cells may occur in *T. corallinae* and *T. pustulatum* var. *macrocarpum* (Fig. 112). Axial filaments often contain floridean starch grains and these are particularly large in *T. pustulatum* var. *macrocarpum* (Figs 98, 104).

Erect filaments

These may be absent or up to about 12 cells long. Their cells are usually vertically elongated and contiguous cells are aligned in most taxa, the 'rows' thus formed tending to be horizontally arranged in var. *macrocarpum* (Fig. 91) but somewhat sinuate in other taxa (e.g. Fig. 66). Secondary pit connections between contiguous cells tend to be more conspicuously tube-like in var. *macrocarpum* than other taxa. In *T. corallinae* (Fig. 214) and *T. laminariae* (Fig. 229) contiguous cells are frequently unaligned.

Surface view

Under the SEM, marginal and other bistratose areas (Fig. 24) show radiating axial filaments composed of radially elongated cells with short epithallial concavities. This surface pattern was first observed in coralline algae by Garbary (1978) and has since been recorded in many taxa, for example in *Fosliella* and *Pneophyllum* (Chamberlain, 1983). In some instances, young, partly calcified thalli were found (Fig. 34) whose structure indicates that the side walls become calcified before the cell roof (cf. Garbary, 1978, fig. 6).

In *T. corallinae* (Fig. 213) and *T. laminariae* (Fig. 236) the superficial arrangement of cells into apparent filaments persists even in thick thalli, but in *T. pustulatum* var. *pustulatum* (e.g. Fig. 27) a honeycomb-like pattern develops on the surface of the mature thallus. In this pattern the calcified side walls of subepithallial initials form a ridge cupping a concavity. An epithallial cell may sometimes be seen in this concavity but usually it has been destroyed or shrunken during processing.

In *T. pustulatum* var. *macrocarpum* cells of mature thalli may develop a smooth, flat top (Figs 30–33) with a minute central protuberance or hole. This is probably the top of a newly developing epithallial cell with the central hole or protuberance marking the pit connection with an epithallial cell that has now been shed (cf. Fig. 32). A somewhat similar structure has been seen in *Clathromorphum reclinatum* (Foslie) Adey (Garbary & Scagel, 1979, fig. 5) and occurs throughout the genus *Leptophytum* in the British Isles (Chamberlain, 1990). This structure has not been seen in any other taxon of *Titanoderma* in the British Isles, but insufficient observations have been made at present to assess its taxonomic significance.

Trichocytes occur quite commonly in *T. pustulatum* var. *confine* (Figs 15, 29) and occasionally in var. *pustulatum,* var. *canellatum*, and var. *macrocarpum* (Fig. 152), but they are not regarded as of diagnostic significance. It is not known whether the segmented calcification sometimes seen in var. *pustulatum* (Figs 28, 73) has any taxonomic significance.

Tetra/bisporangial conceptacles

All British Isles taxa of *Titanoderma* bear bisporangial conceptacles except *T. laminariae* which has tetrasporangial ones. As has been stated, *T. corallinae* (Fig. 52j) and *T. laminariae* (Fig. 52k) are distinguished diagnostically by having more or less entirely immersed conceptacles. The following discussion refers to the *T. pustulatum* complex which has more or less raised conceptacles:

Conceptacle anatomy

Within the four varieties of *T. pustulatum* the anatomical structure of the conceptacle roof in the region of the ostiole shows differential characters. The roof of var. *pustulatum* (Fig. 15a) and var. *canellatum* (Fig. 15i) are both three cells thick throughout with a tall, relatively thin central cell and small epithallial and inner cells. The central cell in var. *canellatum* tends to be somewhat wider and more clavate than that of var. *pustulatum*, but the difference between these varieties depends principally on the absence of erect filaments and the smaller size of var. *canellatum*. Both var. *macrocarpum* and var. *confine* have roofs that are thickened near the ostiole (Figs 15b-h). In var. *confine* the roof is up to four or five cells thick with cells of variable length; the roof filaments of var. *macrocarpum* may be up to seven cells long with the cells being more or less equal in size. Roof anatomy must be used in conjunction with other characters for taxon differentiation because intermediate forms occur. For example the plant in Figure 15c is classified as var. *macrocarpum* on the basis of habit, colour, the size and shape of cells and pit connections, and the horizontal rather than sinuate cell 'rows', but the anatomy of the roof could be interpreted as resembling var. *confine*.

Conceptacle surface

Garbary (1978) showed that the calcification pattern on the roof cells of var. *pustulatum* (as *Dermatolithon pustulatum*) differed distinctively from that of var. *canellatum* (as *D. litorale*) and these two varieties have proved to be consistent in this respect in the British Isles. The roof of var. *pustulatum*

(Figs 36, 37) is smooth in outline and shows an extension of the honeycomb-like thallus surface. The roof of var. *canellatum* (Figs 40, 205) shows a stepped appearance, with the roof cells being heavily calcified on the outer surface and forming a cup holding the epithallial cell more or less at right angles to the conceptacle surface.

Less consistency is seen in var. *confine* and var. *macrocarpum*. Mature conceptacles of var. *confine* (Figs 44, 159) usually show a somewhat ridged structure and those of var. *macrocarpum* (Figs 45, 46) may have horseshoe-like calcification with a minute central hole, presumably where an epithallial cell was previously attached. Both varieties show much variation, however, and stepped roofs (Figs 42, 150, 180) often occur. Developmental stages in roof development may show surface features that differ from the mature structure. During development, for example, layers of epithallial cells are shed from the thallus surface overlying the emerging conceptacle (Figs 38, 41). Furthermore, in young conceptacles bulbous (Figs 48, 123, 162) or stepped (Fig. 42) cell surfaces may develop in the early stages on roofs that may later show honeycomb-like or ridged structures. It is important, therefore, to make observations on mature conceptacles for differential assessment.

The organization of species descriptions

As for *Fosliella* and *Pneophyllum* (Chamberlain, 1978), species descriptions are based mainly on the format recommended for the *Biological flora of the British Isles* (Burrows, 1959). Descriptions of taxa are based on material collected in the British Isles, but detailed descriptions of most of the relevant type specimens are also presented.

A formal diagnosis is not included in descriptions of species or varieties because in effect the relevant information is included in Table 1 and in the keys.

Efforts have been made to refer to British Isles compendia such as Harvey (1849, 1851), Batters (1890, 1902), Holmes & Batters (1891), Knight & Parke (1931), Newton (1931), Parke & Dixon (1976), and Guiry (1978*b*), but despite examining relevant herbarium specimens when available, it has not always been possible to decide exactly to what taxon these authors referred.

Distribution data (Fig. 49) are mainly limited to confirmed records, at least for the rarer species. In common with most algae, the south and west of England and Ireland are the richest areas in both numbers and species and the southern half of the east coast of England the most impoverished.

Voucher specimens collected during this study have been deposited in BM.

Aids to identification

The following aids are provided: a list of substrata with their most frequently occurring *Titanoderma* species or varieties (p. 22); a summary (Table 1, p. 23) of the differential characteristics of the *T. pustulatum* complex; a key to species and varieties based on diagnostic or the most reliable differential characters (p. 24); a key to species and varieties based on characters that can be seen either in the field or under a low power dissection microscope (p. 24); and a composite plate (Fig. 52) illustrating tetra/bisporangial conceptacles of all taxa recognized in the British Isles.

Principal substrata

(all *Titanoderma* varieties pertain to *T. pustulatum*)

Chondrus crispus Stackhouse
  var. *pustulatum*
Corallina officinalis L.
  T. corallinae, var. *confine*
Furcellaria lumbricalis (Hudson) Lamouroux
  var. *confine, T. corallinae*
Gelidium pusillum (Stackhouse) Le Jolis
  var. *confine*, var. *canellatum*
Halopitys incurvus (Hudson) Batters
  var. *confine*
Jania rubens (L.) Lamouroux
  var. *canellatum*
Laurencia pinnatifida (Hudson) Lamouroux
  var. *confine*
Mastocarpus stellatus (Stackhouse in Withering) Guiry in Guiry, West, Kim & Masuda
  var. *pustulatum*
Phyllophora crispa (Hudson) Dixon
  var. *macrocarpum*
Polysiphonia elongata (Hudson) Sprengel
  var. *pustulatum,* var. *confine*
Cystoseira nodicaulis (Withering) Roberts
  var. *confine*
Laminaria digitata (Hudson) Lamouroux and *L. hyperborea* (Gunnerus) Foslie, holdfasts and stipes
  var. *pustulatum, T. laminariae* (easily confused with *Lithophyllum crouanii)*
Cladophora rupestris (L.) Kützing
  var. *canellatum*
Shells, glass, stones, rocks, etc.
  var. *macrocarpum,* var. *confine*, var. *pustulatum* (rarely)

The above records refer to the intertidal zone, but most species also occur in the subtidal, most notably *T. pustulatum* var. *macrocarpum*, the deepest record for which is 70-90 m (Adey, 70-11-A, USNC!).

On rocks it is very easy to confuse mauvish plants of *T. pustulatum* var. *macrocarpum* and var. *pustulatum* with carposporangial plants of *Phymatolithon lenormandii*, and only sectioning can establish the difference.

TAXONOMIC DESCRIPTIONS

Titanoderma Näg. in Näg. & Cramer, *Pfl.-physiol. Unters.* **1**(2): 532 (1858).—*Melobesia* Heydrich in *Ber.dt. bot.Ges.* **15**: 408 (1897) (non *Melobesia* Lamouroux, nec *Melobesia* Foslie).—*Dermatolithon* Foslie in *K.nor. Vidensk. Selsk.Skr.* **1898**(3): 11(1898).—*Lithophyllum* Philippi subgenus *Dermatolithon* (Foslie) Foslie in *K.nor. Vidensk. Selsk.Skr.* **1904**(2): 3 (1904). Type species: *Titanoderma pustulatum* (Lamouroux) Näg. in Näg. & Cramer, *Pfl.-physiol. Unters.* **1**(2): 532 (1858). (see Woelkerling et al. (1985).

Litholepis Foslie in *K.nor. Vidensk.Selsk.Skr.* **1905**(5): 5 (1905).—*Melobesia* Foslie (non Lamouroux nec Heydrich)

Table 1 Characteristic features of four varieties of *Titanoderma pustulatum* in the British Isles

	var. *pustulatum*	var. *macrocarpum*	var. *confine*	var. *canellatum*
Habitat	mainly intertidal	mainly subtidal	mainly intertidal	mainly intertidal
Substratum	epiphytic expecially on *Mastocarpus, Chondrus & Laminaria,* sometimes on rock	on rocks and shells sometimes epiphytic especially on *Phyllophora*	on rocks and shells or epiphytic especially on turf algae & *Furcellaria*	epiphytic especially on *Cladophora, Jania & Gelidium*
Habit & thallus thickness	flat non-imbricating to 370 μm	flat or imbricating to 700 μm	flat or imbricating to 900 μm	flat non-imbricating to 80 μm
Colour (fresh plants)	bright mauve-pink	rose- or salmon pink, reddish or orangish	blueish, violet or mauvish	violet or greyish
Thallus surface (SEM)	honeycomb-like	flat-topped cells or honeycomb-like	honeycomb-like	axial filaments evident
Axial cell shape & orientation (radial VS)	tall, sinuate, oblique	tall, sinuate, oblique to short vertical	tall, sinuate, oblique	tall, sinuate, oblique
Axial cells (VS) h × l	(10) 48 ± 27 (138) × (8) 13 ± 3 (21) n = 101	(5) 55 ± 24 (139) × (9) 20 ± 8 (36) n = 158	(20) 57 ± 25 (117) × (8) 11 ± 2 (14) n = 30	33–91 × 6–7
Erect filaments	to 12 cells	to 14 cells	to 16 cells	absent except near conceptacles
Erect filament cells (VS) l × d	(8) 28 ± 14 (86) × (6) 12 ± 3 (26) n = 133	(5) 39 ± 17 (80) × (9) 17 ± 5 (41) n = 176	(13) 32 ± 14 (78) × (8) 11 ± 2 (14) n = 50	absent
Bisporangial conceptacle shape & external diameter	convex to low hemispherical 400–800 μm	convex, conical or hemispherical 400–900 μm	conical with rounded top 400–500 μm	very prominent rounded to 400 μm
Bisporangial conceptacle periphery (external)	not clearly defined	not or somewhat defined	mainly clearly defined	clearly defined, often skirted
Bisporangial conceptacle chamber shape & size, d × h	low elliptical (156) 363 ± 54 (468) × (78) 138 ± 33 (234) n = 64	low elliptical (190) 400 ± 81 (540) × (78) 124 ± 27 (210) n = 72	elliptical to rounded (234) 305 ± 49 (416) × (91) 171 ± 59 (234) n = 15	rounded 130–350 × 68–215
Bisporangial conceptacle surface (SEM)	honeycomb-like	variously stepped or ridged	mainly irregularly ridged	regularly stepped
Bisporangial conceptacle roof & thickness (VS)	3 cells thick tapering to ostiole (23) 45 ± 9 (73) n = 64	to 7 cells thick, thickening to ostiole (52) 81 ± 9 (104) n = 72	to 4 cells thick, thickening to ostiole (29) 49 ± 9 (62) n = 15	3 cells thick, thickening to ostiole 26–52
Bisporangia l × d	(72) 111 ± 20 (156) × (33) 60 ± 14 (104) n = 73	(50) 70 ± 13 (117) × (21) 39 ± 9 (65) n = 85	(62) 84 ± 13 (104) × (26) 41 ± 8 (52) n = 15	60–75 × 28–36

h = height, l = length, d = diameter (see Figs 50, 51), measurements in μm: (minimum) mean ± standard deviation (maximum), n = sample number of measurements (mean and standard deviation not given for var. *canellatum* because only a small sample was available).

subgenus *Litholepis* (Foslie) Lemoine in *Dansk.bot.Ark.* **3**: 176 (1917).—*Fosliella* Howe subgenus *Litholepis* (Foslie) Cabioch in *Cah.Biol.mar.* **13**: 182 (1972). Type species: *Litholepis caspica* Foslie in *K.nor.Vidensk.Selsk.Skr.* **1905** (5): 5 (1905).

DIAGNOSIS. Plants crustose, dorsiventral, bistratose or developing erect filaments; having a single layer of axial filaments with obliquely orientated, predominantly palisade cells (in VS): within the Lithophylloideae differing from *Lithophyllum* in having predominantly palisade axial cells, and in having a vegetative thallus that is partly or entirely bistratose; from *Ezo* in not being parasitic; from *Tenarea* in not having an isobilaterally organized thallus; relationship to *Goniolithon* not yet determined.

DESCRIPTION. *Thallus* basically dorsiventrally organized, calcified, nongeniculate, crustose, sometimes producing protuberances, mainly epiphytic on algae and marine angiosperms, also epilithic on rocks, stones, etc., or epizoic on shells, entirely or partially attached; in VS single, basal layer of *axial filaments* with cells that are predominantly tall, obliquely orientated, and often sinuate, secondary pit connections numerous, cell fusions normally absent, *thallus margins* and/or regenerating thallus at least partly bistratose, *mature thallus* entirely bistratose, or with *erect filaments* up to 20+ (rarely 90+) cells long, cells usually vertically elongated and horizontally aligned with secondary pit connections two thirds or more of the way up the cells, *epithallial cells* triangular, flattened or domed, *trichocytes* occurring sometimes. *Gametangial plants* monoecious or dioecious; spermatangial

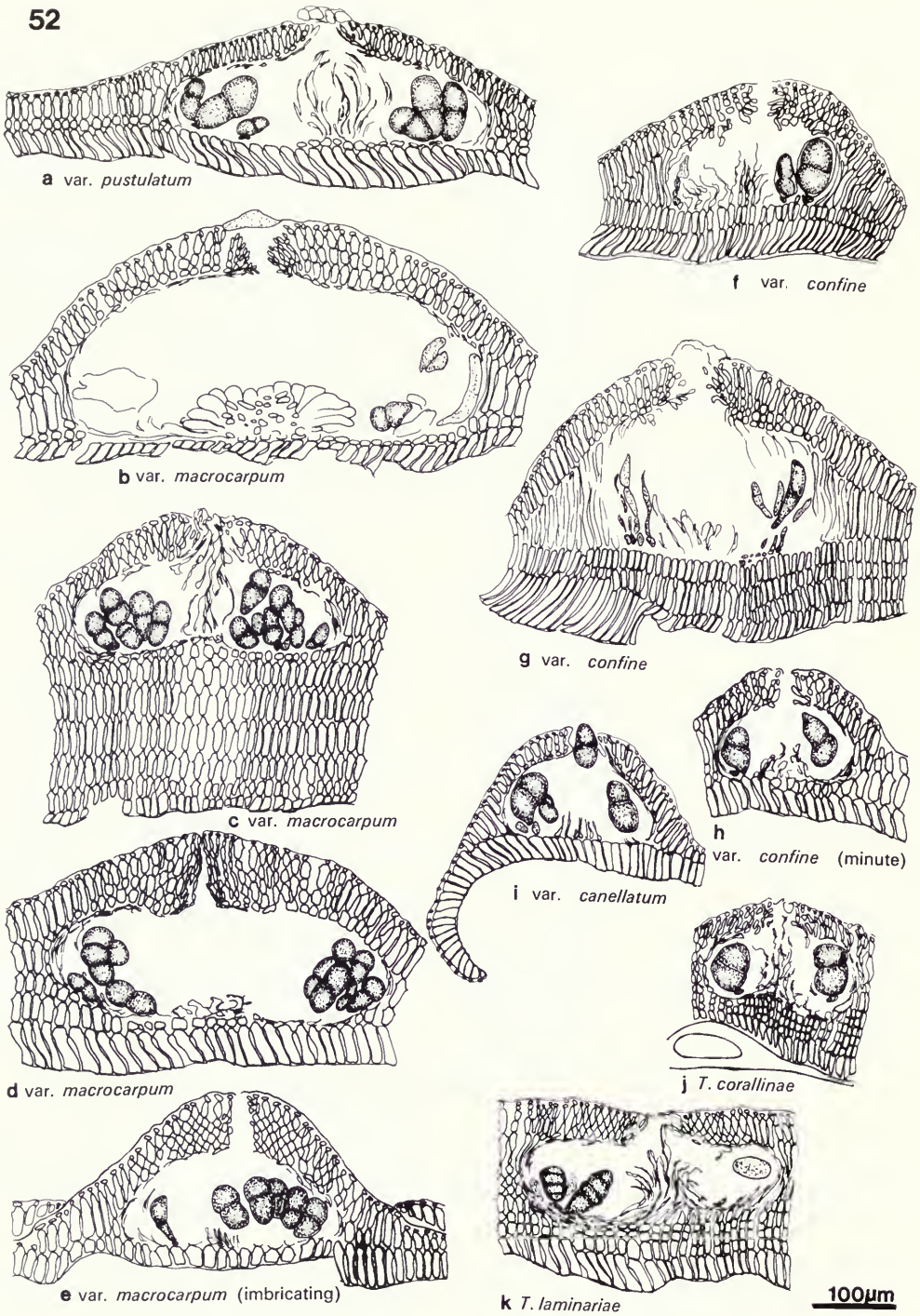


Fig. 52 Vertical sections to show comparative features of tetra/bisporangial conceptacles of British Isles taxa of *Titanoderma*.

a. *T. pustulatum* var. *pustulatum* on *Laminaria* (86/134).
b. *T. pustulatum* var. *macrocarpum*, lectotype specimen (CHE) on *Phyllophora*.
c. *T. pustulatum* var. *macrocarpum*, epilithic (84/229).
d. *T. pustulatum* var. *macrocarpum* on *Laminaria* holdfast (86/159).
e. *T. pustulatum* var. *macrocarpum*, imbricating growth form, epilithic (84/263).
f. *T. pustulatum* var. *confine* on *Furcellaria* (84/28B).
g. *T. pustulatum* var. *confine*, epilithic (84/147).
h. *T. pustulatum* var. *confine*, minute growth form, on *Furcellaria* (79/208).
i. *T. pustulatum* var. *canellatum* on *Gelidium pusillum* (76/193).
j. *T. corallinae* on *Furcellaria* (82/99).
k. *T. laminariae* on *Laminaria* (85/191).

conceptacles originating in subepithallial initials, raised to immersed, spermatangia confined to conceptacle floor, single central ostiole often prolonged into a spout; *carpogonial conceptacles* originating in subepithallial initials, raised to immersed, with central ostiole through which trichogynes protrude, fertile central carpogonial branches bearing one carpogonium; *carposporangial conceptacles* raised to immersed with central continuous fusion cell, central sterile carpogonial branches often becoming conspicuously clavate, gonimoblast filaments borne from extreme periphery or lower surface of periphery of fusion cell, *carposporangia* released through single, central ostiole; *tetra/bisporangial plants* with single-pored conceptacles superficially similar to carposporangial ones, conceptacle primordium originating in subepithallial intitials, roof formed by growth of filaments interspersed among sporangia as well as by centrally located tuft of sterile filaments called a columella, ostiole formed by breakdown of upper part of columella, *tetra/bisporangia* borne on stalk cells in a peripheral ring, tetraspores (as far as is known) haploid, formed by simultaneous zonate division, uninucleate bispores (as far as is known) diploid, binucleate bispores (as far as is known) haploid. *Spore germination disc* with central element of two rows of four cells.

HISTORICAL. Species pertaining to *Titanoderma*, originally classified as *Melobesia* (Lamouroux, 1816), were later included in *Lithophyllum* (e.g. Heydrich, 1897*a*, 1897*b*). Foslie (1898*b*) erected *Dermatolithon* to accommodate species previously classified in *Melobesia* Foslie (non Lamouroux), but unlike that genus, having no columella. He overlooked Nägeli's (1858) earlier publication of *Titanoderma* and this was rectified by Woelkerling et al. (1985). Further historical details are given on pp. 4–11 and in Woelkerling et al. (1985).

TAXONOMY. At least 67 specific and infraspecific taxa have been included in *Titanoderma* (as *Dermatolithon*), many of which require detailed investigation. In addition to the type species, *Melobesia pustulata* Lamouroux, Woelkerling et al. (1985) recombined in *Titanoderma* 10 taxa whose type specimens had been examined by Adey (1970) and five further species they considered to be correctly assigned to the genus. Dawson (1955) drew up a preliminary working key to the living species of *Dermatolithon* in which he included 22 species or formae, some of which would now be included in other genera. Lemoine (1971) drew up a further identification chart in which she added a few species to Dawson's (1955) list; she further commented that there were probably as many species again in the fossil flora.

DISTRIBUTION. *Titanoderma* is known from all warm to cold temperate and tropical waters. It is possibly absent from polar waters, but occurs at least as far south as southern Argentina (Mendoza, 1977).

Key to *Titanoderma* in the British Isles

(For use on fresh or preserved material and including microscopic characters)

1 Conceptacles immersed in the thallus 2
Conceptacles raised (*T. pustulatum*) 3

2(1) Tetrasporangial conceptacle chambers over 300 µm diameter ..... 3. **laminariae** (p.69)
Bisporangial conceptacle chambers under 250 µm diameter ..... 2. **corallinae** (p. 66)

3(1) Conceptacle roofs three cells thick, small upper and lower cells, tall central cell 4
Conceptacle roofs more than three cells thick 5

4(3) Conceptacles gradually raised, usually over 500 µm external diameter ..... 1a. **pustulatum** var. **pustulatum** (p. 26)
Conceptacles abruptly prominent, under 400 µm external diameter ..... 1d. **pustulatum** var. **canellatum** (p. 61)

5(3) Erect filaments absent, plants composed of imbricating lobes ..... 1b. **pustulatum** var. **macrocarpum** (p. 33)
..... (imbricating growth form)
Erect filaments present 6

6(5) Conceptacles mainly abruptly prominent, rounded-conical, roofs to four cells thick with cells irregularly sized, axial cells tall, thin, and oblique, erect cells 11±2 µm diameter, plants blueish/violet ..... 1c. **pustulatum** var. **confine** (p. 50)
Conceptacles raised to broadly prominent, roofs usually more than four cells thick with cells more or less equally sized, areas of short, wide, vertically orientated axial cells often present, erect cells 17±5 µm diameter, plants orange-pink to mauvish ..... 1b. **pustulatum** var. **macrocarpum** (p. 33)

Field key to *Titanoderma* in the British Isles

(For use on freshly-collected material and with the use of a dissection microscope)

1 Thallus flat, mainly with thickened (not attenuated) margin, conceptacles flush with thallus surface or slightly raised 2
Thallus varying from flat to imbricating with attenuated margin, conceptacles raised to prominent (*T. pustulatum*) 3

2(1) Growing on *Laminaria* stipes and holdfasts ..... 3. **laminariae**[1] (p. 69)
Growing mainly on *Corallina* and *Furcellaria*, occasionally on other red algae (not observed on *Laminaria*). ..... 2. **corallinae** (p. 66)

3(1) On rocks, stones, and shells 4
Epiphytic 5

4(3) Thalli sometimes flat, usually imbricating, blueish/violet, conceptacles usually abruptly emergent, conical with rounded top, not exceeding 500 µm diameter, mainly intertidal ..... 1c. **pustulatum** var. **confine** (p. 50)
Thalli flat to imbricating, orange-pink to mauvish, conceptacles gradually to abruptly emergent, shallowly conical to hemispherical, usually exceeding 500 µm external diameter, mainly subtidal or in low intertidal pools ..... 1b. **pustulatum** var. **macrocarpum**[2] (p. 33)

5(3) Thalli very thin, flat, pinkish or greyish, conceptacles abruptly emergent, hemispherical, often with a skirt at base, not usually exceeding 300 µm external diameter, mainly on *Cladophora, Jania* or *Gelidium pusillum*, intertidal ..... 1d. **pustulatum** var. **canellatum**[3] (p. 61)
Thalli thicker, blueish, mauve-pink or brown-pink, conceptacles mainly exceeding 300 µm external diameter 6

6(5) Thalli flat, mauve-pink or brown-pink, conceptacles gradually emergent, somewhat raised or domed, usually exceeding 500 µm external diameter, mainly on *Chondrus, Mastocarpus* or *Laminaria* (often overgrowing *Melobesia membranacea*), also on other red and brown algae, mainly intertidal ..... 1a. **pustulatum** var. **pustulatum**[4] (p. 26)
Thalli sometimes flat, usually imbricating, blueish, conceptacles usually abruptly emergent, conical with rounded top, not exceeding 500 µm external diameter, mainly on turf algae, *Laurencia*

pinnatifida or *Furcellaria*, intertidal and subtidal..... ..... 1c. **pustulatum** var. **confine** (p. 50)

[1] On *Laminaria* it is often difficult to distinguish *T. laminariae* from *Lithophyllum crouanii*; when fertile the conceptacles (all types) of *L. crouanii* are evident as white circles, those of *T. laminariae* are located only by the presence of ostioles. To be sure of identification, section thallus to determine the presence (*Titanoderma*) or absence (*Lithophyllum*) of palisade cells.
[2] Occasionally epiphytic on *Phyllophora* and indistinguishable from var. *pustulatum* except on the basis of roof structure in VS.
[3] Distinguished by its complete lack of erect filaments from the small growth form of var. *confine*.
[4] Rarely on rocks or shells, when it can only reliably be distinguished from var. *macrocarpum* on the basis of roof structure in VS.

1. **Titanoderma pustulatum** (Lamouroux) Näg.—*Melobesia pustulata* Lamouroux, *Hist. polyp. corall.*: 315 (1816).—*Titanoderma pustulatum* Näg. in Naeg. & Cramer, *Pfl.-physiol. Unters.* **1**(2): 532 (1858).—*Dermatolithon pustulatum* (Lamouroux) Foslie in *K.nor. Vidensk. Selsk.Skr.* **1898**(3): 11 (1898).—*Lithophyllum pustulatum* (Lamouroux) Foslie in *K.nor. Vidensk. Selsk. Skr.* **1904**(2): 8 (1904).—*Epilithon pustulatum* (Lamouroux) Lemoine in *Bull. Soc. linn.Provence* **3**: 10 (1921), in error—pers.comm. (Art. 34.1).— *Tenarea pustulata* (Lamouroux) W. Adey, in *Colo.Sch.Mines Q.* **60**(2): 88 (1965), invalid. (Art. 33.2). Type: France, Hb. Lamouroux, on *Chondrus crispus* (CN!—lectotype, see Woelkerling et al., 1985).

1a. var. **pustulatum**
Figs 52a, 53, 54–81.

Dermatolithon macrocarpum f. *faeroensis* Foslie in *K.nor. Vidensk.Selsk.Skr.* **1899**(7): 14 (1900).—*Lithophyllum pustulatum* f. *macrocarpa* Foslie in *K.nor. Vidensk. Selsk. Skr.* **1905**(3): 117 (1905).—*Lithophyllum macrocarpum* f. *faeroensis* Foslie in *K.nor. Vidensk. Selsk.Skr.* **1905**(3): 128 (1905). [Foslie applied these two names to the taxon in the same paper]. Type: as *Lithophyllum macrocarpum*, Faeroes, Bodring, 18.15/11.97, on *Gigartina mamillosa*, H. Jønsson, F. Børgesen, 284 (TRH!—lectotype selected here). (Fig. 81).

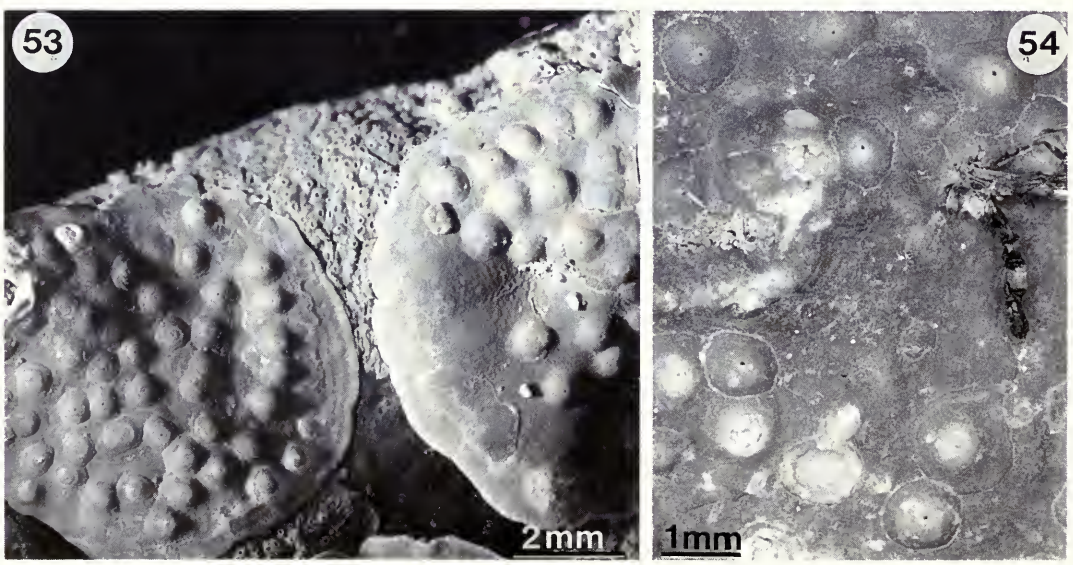
ILLUSTRATIONS. As *Melobesia pustulata,* Lamouroux, *Hist. polyp. corall.*: pl. XII, fig. 2 (1816); as *Dermatolithon pustulatum,* Kornmann, P. & Sahling, P.-H., *Meeresalg. Helgoland:* fig. 115 (1977); as *Titanoderma pustulatum,* Woelkerling et al. in *Phycologia* **24**: figs 29–39 (note that the scale in figs 30, 31, 33, 34 & 35 should read half the stated figure, e.g. fig. 31 should read 10 μm not 20 μm) (1985).

[A note on published records of *T. pustulatum* var. *pustulatum* from the British Isles:

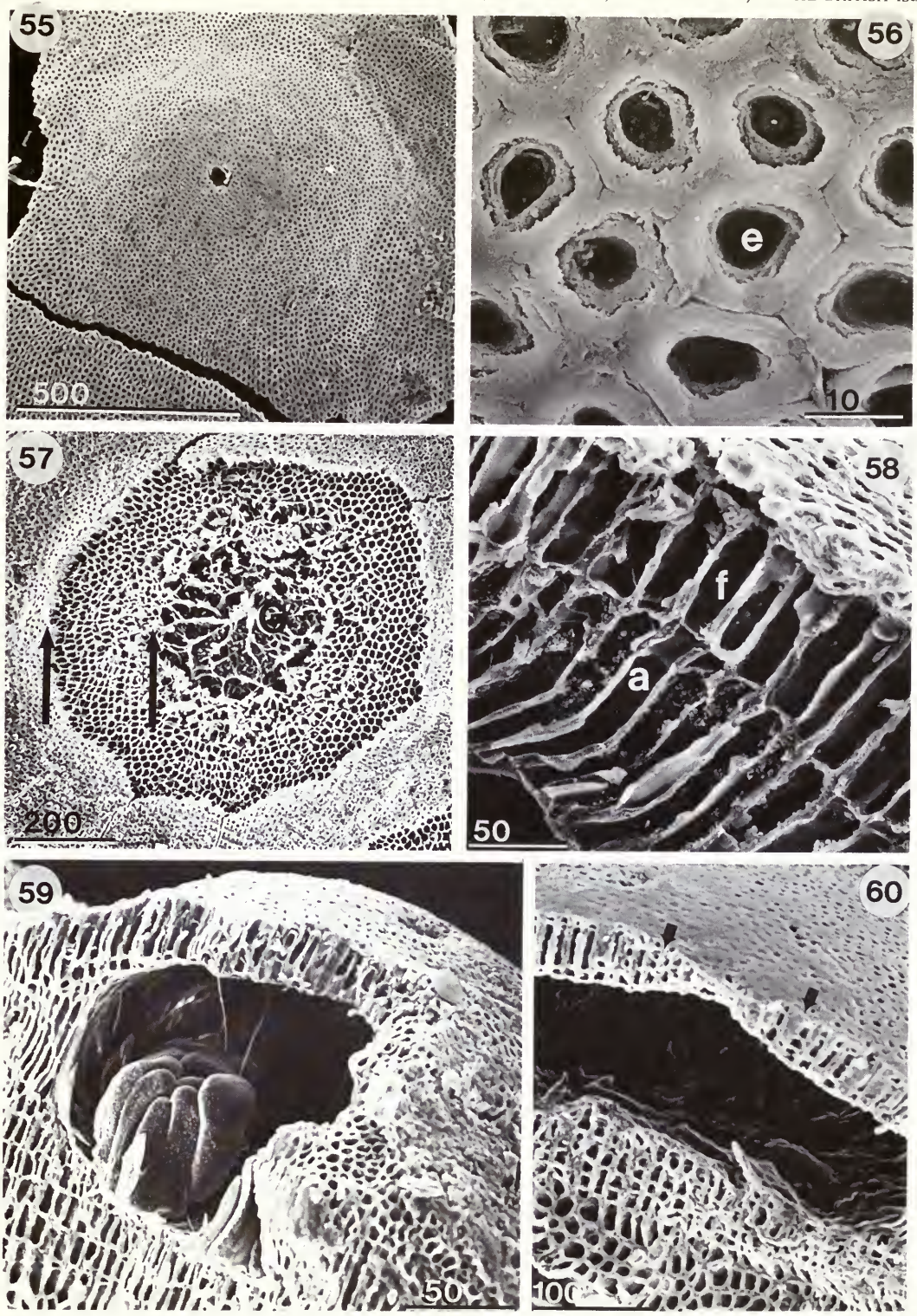
Harvey (1849: 109) recorded *Melobesia pustulata* growing on *Phyllophora rubens, Chondrus crispus*, etc. in the British Isles and later figured the species growing on *Phyllophora rubens* (Harvey, 1851: pl. 347D). This almost certainly represents true var. *pustulatum,* but no specimens substantiating Harvey's records appear to be extant. Harvey (1849) pointed out that *M. pustulata* was among the species considered by Johnston (1842: 220) to be imperfect stages of *Corallina officinalis*.

Titanoderma pustulatum var. *pustulatum* has subsequently been widely reported in the British Isles (e.g. Batters, 1890, as *Melobesia pustulata* and *M. macrocarpa*, 1902, as *Dermatolithon;* Lemoine, 1913*b*, as *Lithophyllum*; Newton, 1931, as *L. pustulatum* and var. *laminariae*; Parke & Dixon, 1976, as *Dermatolithon*; Guiry, 1978*b*, as *Lithophyllum* and *Dermatolithon*) but apart from the drawings by Lemoine (1913*b*: 139) of an unspecified plant, the only illustrations are those in Newton (1931: 305, fig. 188) of which only figure F can be identified and that is a reproduction of Rosanoff's (1866) figure of *Melobesia macrocarpa* (now *T. pustulatum* var. *macrocarpum*).

Nevertheless, var. *pustulatum* is such an abundant and characteristic epiphyte of *Chondrus crispus*, *Mastocarpus stellatus*, and other foliose red algae, that identifications which have been checked (BM and BM-K) have proved to be correct with the exception of a specimen collected at Pridmouth by Tellam (24 May 1886, on *Phyllophora*) which is var. *macrocarpum*. However, the only actual specimens quoted in literature are those collected by Cotton (1912) in the Clare

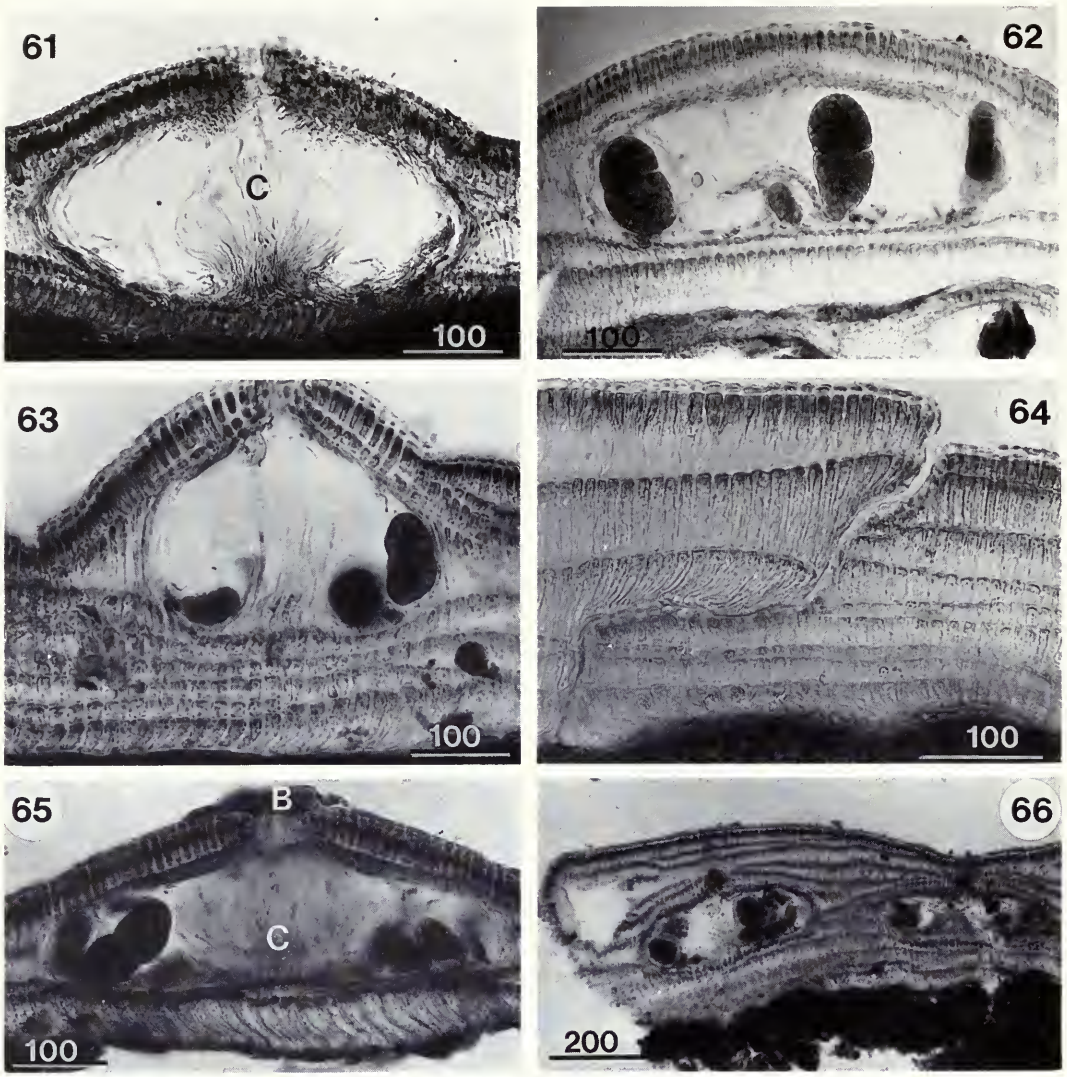


Figs 53–54 External appearance of *Titanoderma*.
53. *T. pustulatum* var. *pustulatum* overgrowing *Melobesia membranacea* on *Chondrus crispus* (88/126).
54. *T. pustulatum* var. *macrocarpum* growing on rock (87/13).



Figs 55–60 Scanning electron micrographs of *Titanoderma pustulatum* var. *pustulatum* (scales in μm).

55. Bisporangial conceptacle (86/147) growing on *Chondrus*.
56. Roof surface of conceptacle in Fig. 55. Heavy calcified ridges surround epithallial concavities (e).
57. Surface view of bisporangial conceptacle (79/76). The roof has broken off showing the broad ring (between arrows) over which the roof was attached. Remnants of a columella (c) remain in the conceptacle centre.
58. Vertical fracture of thallus (84/46) showing tall erect filament cells (f) and sinuate axial cells (a).
59. Vertical fracture of bisporgangial conceptacle (76/44) to show bisporangia in situ.
60. Vertical fracture of bisporangial conceptacle from Børgesen's plant (identified as *Dermatolithon hapalidioides*) from the Faeroes. The roof does not thicken in the centre but roof filaments may be four or five cells long (arrows).



Figs 61–66 Vertical sections of *Titanoderma pustulatum* var. *pustulatum* to show conceptacle and thallus features (scales in μm).
61. To show a prominent columella (c) (86/139).
62. Pear-shaped bisporangium (b) in plant overgrowing *Melobesia membranacea* (M).
63. A very prominent conceptacle (86/130).
64. Two adjacent thalli of thick plants which lack a bistratose margin at their confluence (85/27).
65. Plant growing on *Laminaria hyperborea*. This has a prominent columella (c) and a released bisporangium (B) is blocking the ostiole (86/134).
66. Thick plant showing buried conceptacles (86/129).

Island Survey and identified by Lemoine (1913*b*). Of these, the specimen on *Gigartina* is var. *pustulatum* and that on *Laminaria cloustonii* (*L. hyperborea*) is a mixture of *Phymatolithon* sp. and *Lithophyllum crouanii*. The specimen on *Cladophora rupestris* has not been found. Considerable care needs to be taken when identifying coralline epiphytes on *Laminaria* because, in addition to the above, *T. laminariae* can also be confused with var. *pustulatum* in this situation. Newton (1931: 306) records *Lithophyllum pustulatum* var. *laminariae* which is probably mainly var. *pustulatum*.]

DESCRIPTION. Plants mainly epiphytic, closely adherent, flat and non-imbricating, to 30 mm diameter, 500 μm thick, tapering to an often extensive, bistratose margin, adjoining plants not overgrowing one another, bright mauve-pink to brown-pink (Methuen greyish ruby to dark magenta), chalky, surface smooth. Single layer of *axial filaments* with cells obliquely orientated and usually sinuate, cells 13–190 μm high × 8–21 μm diameter, *erect filaments* absent or to 12 cells long, cells 8–118 μm long × 6–22 μm diameter, *epithallial cells* triangular or domed, thallus cell cytoplasmic contents usually very sparse, starch grains uncommon, trichocytes observed very rarely. *Gametangial and tetrasporangial plants* not seen; *bisporangial conceptacles* widely spaced to densely crowded, raised, arising gradually not abruptly from thallus surface, 400–800 μm external diameter, conceptacle surface honeycomb-like, conceptacle chamber low-elliptical, 156–468 μm diameter, 78–234 μ high, roof 23–73 μm thick, roof three cell layers thick throughout, epithallial and inner cells small, middle cell tall and thin, roof tapering to ostiole, columella

Table 2 To show the first publication by Foslie of formae of *Titanoderma* (as *Lithophyllum* or *Dermatolithon*) and their current names

NAME OF FORMA	DATE	CURRENT NAME
L. pustulatum f. ascripticia	1907*b*: 34	*T. pustulatum* var. *confine*
L. pustulatum f. corallinae	1905*a*: 118	*T. corallinae*
D. pustulatum f. crinita	1900*b*: 21	Type not found
D. macrocarpum f. faeroensis	1900*a*: 15	*T. pustulatim* var. *pustulatum*
L. pustulatum f. intermedia	1905*a*: 117	*T. pustulatum* var. *confine*
D. macrocarpum f. laminariae pro parte	1900*b*: 22	*T. laminariae*
D. macrocarpum f. laminariae pro parte	1900*b*: 22	*T. pustulatum* var. *pustulatum*
D. pustulatum f. macrocarpa	1898*b*: 11	*T. pustulatum* var. *macrocarpum*
L. pustulatum f. similis	1909 : 47	Type not seen

slightly- to well-developed, up to *c.*60 bisporangia, 72–156 μm long × 33–104 μm diameter, old conceptacles usually being in-filled but sometimes becoming buried in thallus.

HISTORICAL. *Titanoderma pustulatum* var. *pustulatum* was originally described by Lamouroux (1816, as *Melobesia*) as a zoophyte (plant-like animal) having a convex, orbicular disc ('plaque') with conceptacles ('cellules') prominent and visible with the naked eye. Only one collection of var. *pustulatum* is present in Lamouroux's herbarium and this has been designated lectotype (Woelkerling et al., 1985). The plant is epiphytic on *Chondrus crispus* and shows the following features: a thallus with tall, sinuate axial cells; erect filaments composed of up to five elongated cells; raised conceptacles (no spores surviving) about 400 μm internal diameter; conceptacle roofs two to three cells deep of which the subepithallial cell is relatively tall and thin; and a honeycomb-like conceptacle roof surface with a large, central ostiole.

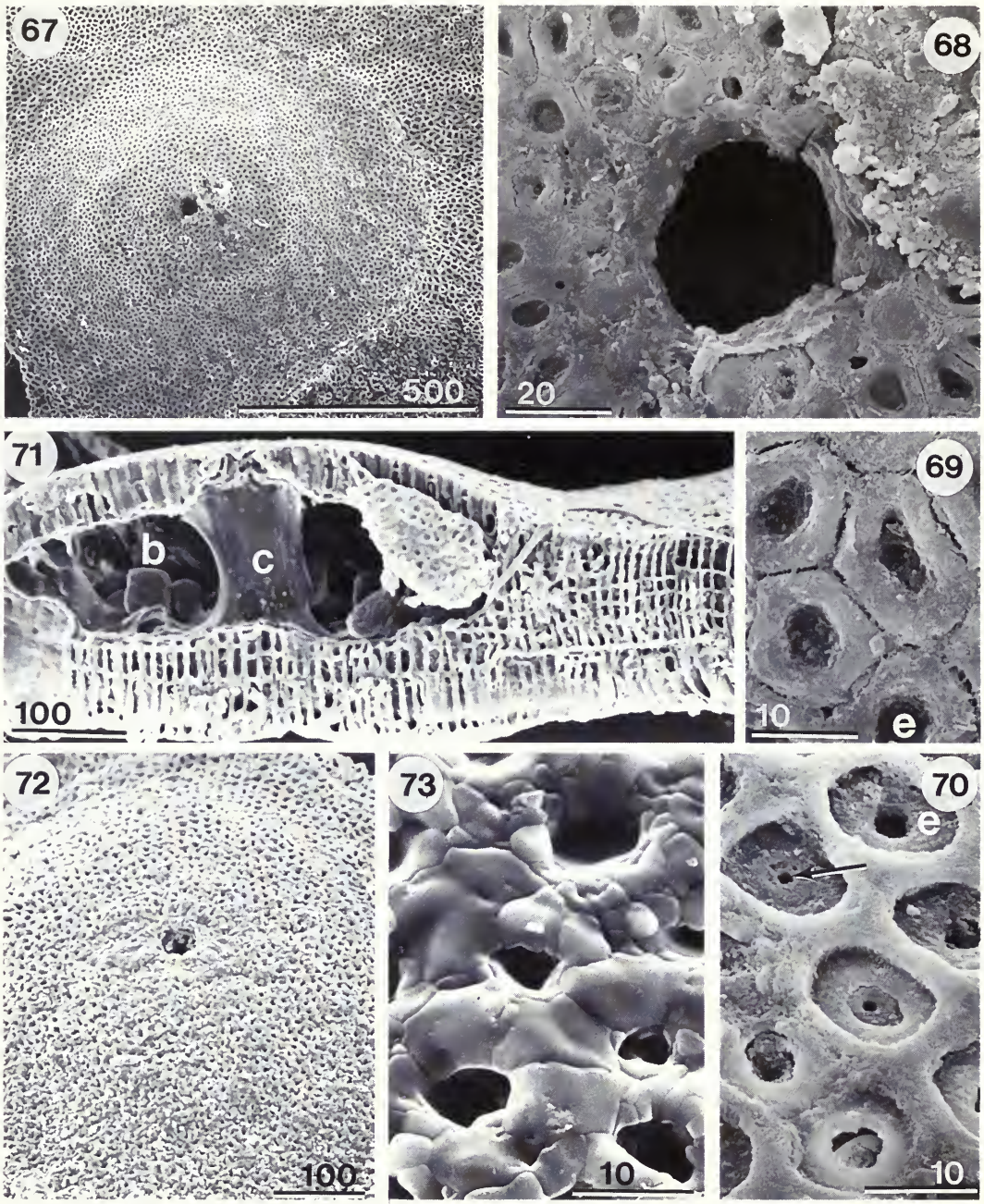
Kützing (1845: 295) recorded var. *pustulatum* (as *Melobesia pustulata*) from the Adriatic. No specimens identifiable as var. *pustulatum* from the Adriatic have been found in Kützing's herbarium but his specimen collected by Meneghini at Livorno is var. *macrocarpum* (L 940.317.500!) while a specimen growing on *Sargassum linifolium* in the Mediterranean (L 940.317.501!) comprises a mixture of *Fosliella* spp. and var. *canellatum*. Kützing (1849: 696) described a new taxon, *Melobesia pustulata* β *canellata,* growing on *Ceramium rubrum* and *Cryptacantha squarrosa* in the Mediterranean. Both of these specimens are now referred to var. *canellatum*. Rosanoff (1866: 73, 74), apparently without seeing Kützing's specimens, considered β *canellata* to represent a form of var. *pustulatum* growing on a terete host and further said that Le Jolis had collected similar material on *Gelidium pusillum*; he appears, however, to have been referring to Le Jolis, Alg. Mar.Cherbourg 275 (CHE!) which is var. *confine*.

Rosanoff (1866) discussed var. *pustulatum* (as *Melobesia pustulata*) although he did not record having examined Lamouroux's material. He concluded that var. *pustulatum* was a species with quite prominent conceptacles which were tetrasporangial; he distinguished it from a new species, *Melobesia macrocarpa,* which had larger and more prominent conceptacles which were bisporangial. In what was to be the only illustration of a *Titanoderma* conceptacle for many years, Rosanoff (1866: pl. IV, fig. 15) accurately showed the multilayered conceptacle roof, robust bisporangia, and relatively broad (compared with var. *pustulatum*) axial cells of var. *macrocarpum* (see Chamberlain, 1986). He did not, unfortunately, illustrate var. *pustulatum* in the same way, showing only two young plants (Rosanoff, 1866: pl. IV, figs 2, 3); however, examination of the specimens in Cherbourg cited as var. *pustulatum* by Rosanoff (1866: 74) showed a mixture of species: var. *canellatum* occurred most frequently, but var. *pustulatum*, var. *confine*, and *Pneophyllum limitatum* (Foslie) Y. Chamberlain were also present.

Foslie discussed var. *pustulatum* in a number of publications, classifying it variously under *Dermatolithon* (Foslie, 1898*b*: 11; 1909: 58) and *Lithophyllum* (Foslie, 1904: 8). He was particularly concerned as to its relationship with var. *macrocarpum*. Apparently without examining the type specimen of either taxon, he discussed them both at length in *Remarks on northern lithothamnia* (Foslie, 1905*a*: 117–128) where, in a final conclusion (there were various intermediate conclusions), on page 127, he proposed that *Lithophyllum pustulatum* was a more southerly species which did not occur north of Cherbourg and the south of the British Isles, while *L. macrocarpum* was distributed northwards from Cherbourg. Foslie described various formae, including f. *faeroensis* (Fig. 81), under the two species and these are shown with their current identification in Table 2. Foslie's discussions on this particular subject are a good example of his style, they jump from one conjecture to another, settle on no particular, soundly based, anatomical features to characterize the species and theorize without benefit of typification. In general, apart from the formae shown in Table 2, it seems that his concept of *Lithophyllum pustulatum* was of a relatively small species, the examples of which would mostly be referable to var. *canellatum*, while *L. macrocarpum* embraced both var. *macrocarpum* and var. *pustulatum*. As shown in Table 3 (p. 31), the identification of var. *pustulatum* also became entangled with *Titanoderma laminariae* (q.v.) and *Lithophyllum crouanii* in Foslie's works.

After Foslie, the next main development was the record by Rosenvinge (1917: 268) of a small fragment of a *Titanoderma* (as *Lithophyllum*) growing on *Corallina officinalis* in the Kattegat which he queried as a form of *L. pustulatum*. Rosenvinge emphasized and illustrated the deep conceptacle roof, particularly round the ostiole, and this feature was later highlighted in Suneson's (1943: 39–43) illustrated account of specimens from Sweden. Again without examining the type specimen, Suneson referred this species to *Lithophyllum pustulatum* (now var. *pustulatum*), but the conceptacle roof structure clearly contradicts that identification and Suneson's material represents a different entity now included in var. *macrocarpum*. Since 1943, Suneson's work has been accepted as the standard of var. *pustulatum* (e.g. Kylin, 1944, 1956; Hamel & Lemoine, 1953), but the records of the species embrace both var. *pustulatum*, and var. *macrocarpum* and it was not until the type specimen of *T. pustulatum* was examined (Woelkerling et al., 1985) that an anatomical basis for distinguishing the taxa was finally established.

PLANT APPEARANCE. Most characteristically var. *pustulatum* (Fig. 53) forms robust, bright mauve-pink thalli (Methuen—greyish ruby) on red algae such as *Chondrus crispus* and *Mastocarpus stellatus*. It also occurs commonly on the stipes and holdfasts of *Laminaria* where it is usually a somewhat



Figs 67–73 Scanning electron micrographs of *Titanoderma pustulatum* var. *pustulatum* growing on *Laminaria* (scales in μm).
67. Bisporangial conceptacle (86/129).
68. Ostiole of conceptacle in Fig. 67.
69 & 70. Younger and older cells from the roof surface of Fig. 67. Both have wide, calcified ridges surrounding epithallial concavities (e), in Fig. 69 the epithallial cells remain but in Fig. 70 they have been destroyed to reveal the pit connection (arrow) with the subtending initial.
71. Vertical fracture of bisporangial conceptacle (83/225), Note the slightly raised roof, strong columella (c) and peripheral bisporangia (b).
72 & 73. Unusual bisporangial conceptacle (73) with roof cells (74) entirely covered by a heavy, calcified deposit apparently laid down in segments (cf. Fig.28) (84/150).

darker, mauve-brown (Methuen—dark magenta), as are plants growing on shells and rocks. On plant hosts it frequently overgrows *Melobesia membranacea* (Esper) Lamouroux. Plants of var. *pustulatum* are closely adherent, up to about 30 mm diameter and 500 μm thick. A slight ridge may form between adjacent thalli but they do not become superimposed; the thallus margin may, however, become detached from the host to give a somewhat leafy appearance particularly when growing on terete plants such as *Cladostephus spongiosus* (Hudson) Agardh. The thallus becomes pale and fragile on drying, crumbles easily and falls off the host. The thallus usually has an extensive non-reproductive margin with a

down-curving calcareous shield (Figs 25, 26) at the outermost edge. In surface view, the young thallus (Fig. 24) is composed of radiating, calcified axial filaments with elongated cells and squarish to rounded epithallial concavities. Older thallus surfaces show honeycomb-like ridges surrounding large epithallial concavities (Fig. 27). Trichocytes have occasionally been seen on SEM preparations (Fig. 35).

Mature bisporangial conceptacles (Figs 36, 53, 55, 67) are raised-domed, emerging gradually rather than abruptly from the thallus surface. Older conceptacles usually become infilled but may become partially or entirely buried in the thallus (Fig. 74) in thick plants. The conceptacle roof has a smooth surface composed of a calcified honeycomb-like framework with rounded epithallial concavities (Figs 37, 56, 68–70, 77) that is similar to the thallus surface; there is a large, central ostiole (Figs 39, 68). Younger conceptacles show bulbous calcification (Fig. 38) and strips of sloughed epithallial tissue often remain. One conceptacle (Figs 72, 73) was seen in which the thallus and roof cells were coated with a thick, segmented calcareous deposit, also observed once on the thallus surface (Fig. 28).

Further consideration of variation in var. *pustulatum* is presented under variation range (see below).

VEGETATIVE ANATOMY. A characteristic feature of a vertical section of var. *pustulatum* is usually the paleness of the thallus cells (Fig. 64). Cytoplasmic contents are sparse and mainly located in the upper parts of the cells (cf. Rosanoff, 1866: 73); starch grains are sometimes present in lower cells. The thallus margin (Fig. 9) usually has a more or less extensive zone composed of axial and triangular epithallial cells only, but in thick plants, such as many seen in Scotland, abutting thalli may have very thick margins (Fig. 64). Axial filaments (Figs 9, 10, 58, 65) are composed of tall, sinuate (in radial VS) cells which vary considerably in height (Table 1) depending on the microscopic features of the substratum (Fig. 19). Axial cells are characteristically swollen at the top and bottom (Fig. 9). Successive axial cells are joined by primary pit connections and as the cells mature further pit connections often develop below the first one (Fig. 9). Cells of erect filaments (Figs 10, 11, 58, 63, 64) are mostly elongated and the end walls of adjacent cells are aligned so that they create up to twelve horizontal rows of cells which vary in height along the row giving a sinuate effect (Fig. 64). Successive cells of erect filaments are connected by primary, and contiguous cells of adjacent filaments by secondary pit connections (Fig. 10).

Epithallial cells occur singly and are triangular at the thallus margin (Fig. 9) but flattened or dome-shaped (depending on the plane of the section) in older parts (Fig. 13).

BISPORANGIAL PLANTS. The development of the bisporangial conceptacle of var. *pustulatum* (Figs 19–23) is described on page 18. The mature conceptacle (Figs 23, 52a, 53–55, 59, 61–63, 65, 67) is characteristically domed and, as can be seen from the thallus surface (Fig. 57), the roof is attached across a wide ring of thallus cells which explains why the roof emerges gradually from the thallus surface rather than abruptly as is seen, for example, in the conceptacles of var. *confine* and var. *canellatum*. In the thicker forms of var. *pustulatum* conceptacles may be only slightly raised (Figs 74–76), becoming flattened as they gradually become immersed in the thallus (Fig. 66).

A diagnostic feature of var. *pustulatum* is the presence of a conceptacle roof that is three cells thick in VS (Figs 23, 52a, 63, 65, 78–80); it comprises a middle cell that is characteristically tall, a domed epithallial cell externally, and a more or less isodiametric cell internally that usually disintegrates in older conceptacles. In thick specimens of var. *pustulatum*, the three-celled roof may not be evident in conceptacles becoming immersed, but it can usually be seen in conceptacles from younger parts of the thallus. A columella always occurs in var. *pustulatum*, it varies widely from a conspicuous, bushy structure (Figs 61, 65, 71) to being very sparse (Figs 23, 63). Bisporangia (Figs 23, 52a, 59, 62) vary considerably in size (Table 1) but are among the largest recorded in the genus. They appear to mature successively so that younger conceptacles seem to have few sporangia; mature conceptacles may be packed with farctate sporangia which easily fall out during sectioning. Mature sporangia are often pear-shaped with the broad end uppermost; there appear to be up to about 60 sporangia per conceptacle. Very occasional tetrasporangia were observed within predominantly bisporangial conceptacles, they were much the same size as the bisporangia.

Table 3 To show the names previously attributed to *Titanoderma laminariae*, *T. pustulatum* var. *pustulatum* and *Lithophyllum crouanii*.

Taxon / Author	*Titanoderma laminariae*	*T. pustulatum* var. *pustulatum*	*Lithophyllum crouanii*
Holmes, 1883	*Melobesia laminariae*		*Melobesia laminariae*
Foslie, 1898*c*	*M. laminariae* pro parte (as to Le Jolis 255)		*L. crouanii*
Foslie, 1900*a*	*Dermatolithon laminariae*		*L. crouanii*
Foslie, 1900*b*	*D. macrocarpum f. laminariae*	*D. pustulatum f. typica*	*L. crouanii*
Foslie, 1905*a*	*L. pustulatum* pro parte	*L. pustulatum f. laminariae* pro parte	*L. crouanii* pro parte
	L. crouanii pro parte		
Batters, 1890	*M. laminariae*	*M. laminariae*	*M. laminariae*
Batters, 1902	*D. macrocarpum f. laminariae*	*D. pustulatum*	*D. macrocarpum f. laminariae*
Newton, 1931	*L. crouanii* pro parte	*L. pustulatum* var. *laminariae*	*L. crouanii* pro parte
Hamel & Lemoine, 1953	*D. crouanii*	*D. pustulatum f. laminariae*	
Adey & Adey, 1973			*L. orbiculatum*

VARIATION RANGE. In the absence of any perceived diagnostic characters, the wide variation in var. *pustulatum* has led to much taxonomic confusion. The following types of plant all have the diagnostic characteristics of a raised, three-celled bisporangial conceptacle roof that tapers towards the ostiole and honeycomb-like roof surface, but they differ sufficiently in appearance to have caused uncertainty:

(a) Bright mauve-pink plants growing on *Chondrus* and *Mastocarpus* (Fig. 53) with raised conceptacles that have elliptical chambers. Such plants resemble the type material and are very common.

(b) Mauvish, usually rather thin plants growing on *Laminaria* spp. stipes and holdfasts. These differ from a) in being darker

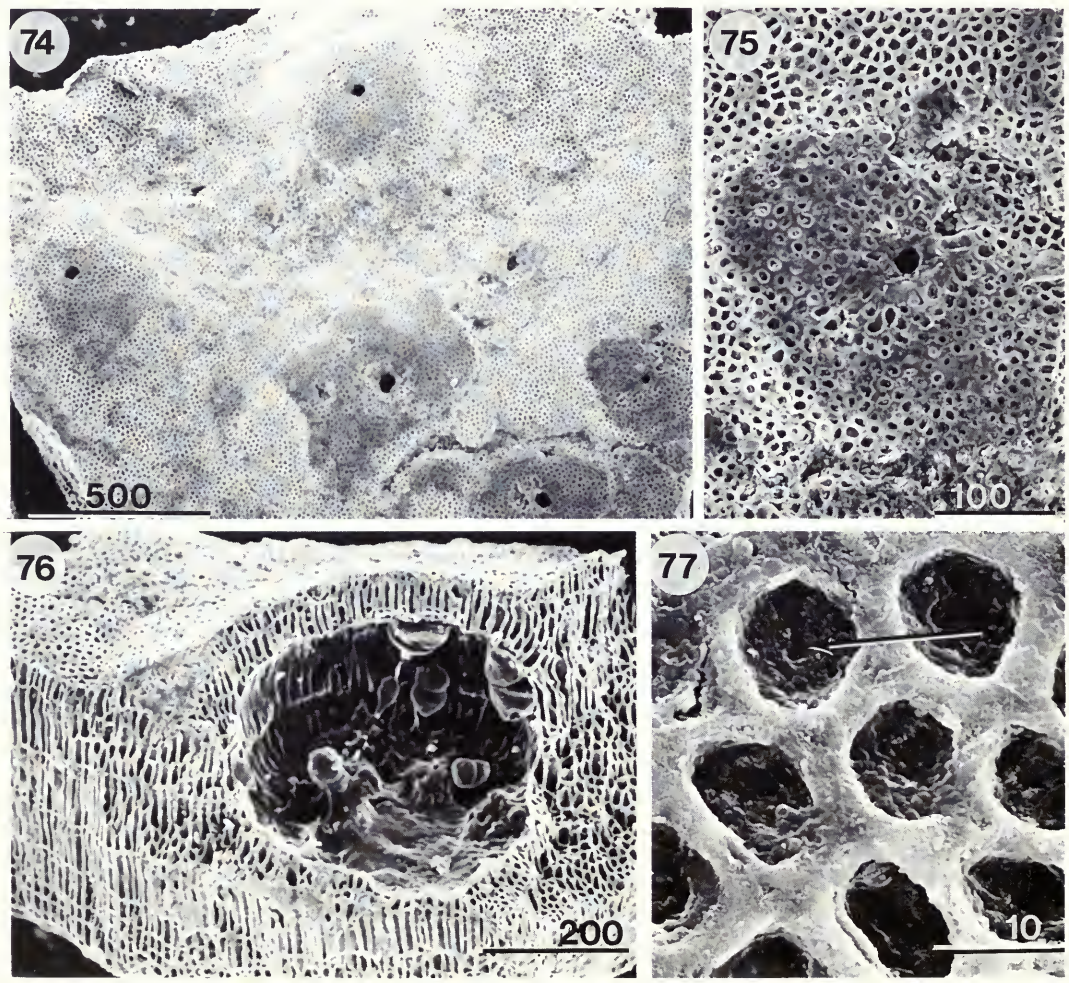
in colour and having low-triangular conceptacle chambers (Figs 52a, 65, 71). Such plants have come to be known as *Dermatolithon pustulatum* f. *laminariae* (Newton, 1931—as *Lithophyllum*; Hamel & Lemoine, 1953) although historically this name is interwoven with *T. laminariae* and *Lithophyllum crouanii* (Table 3). Kornmann & Sahling (1977: 206, as *Dermatolithon pustulatum*) describe this form in some detail.

(c) Plants with a thick thallus (Fig. 74) in which old conceptacles become buried. Such plants are found particularly on *Laminaria* holdfasts in Scotland and northern England. They correspond to plants described by Foslie (1900*a*: 4) as *Dermatolithon macrocarpum* f. *faeroensis*, the lectotype (TRH!) of which has been examined, as has further material in TRH and specimens collected recently in the Faeroes. Both the lectotype of f. *faeroensis* and the plant growing on a limpet which is the basis of Børgesen's (1903) record of *Dermatolithon hapalidioides* in the Faeroes, may have a roof composed of four small cells near the ostiole (Fig. 81) as is seen occasionally in plants from the British Isles.

(d) Epilithic and epizoic plants that are usually dark in colour and may have raised, non-burying conceptacles, but plants with immersed old conceptacles have been found on subtidal stones (Fig. 66). Such plants are almost impossible to distinguish externally from var. *macrocarpum* on similar substrata.

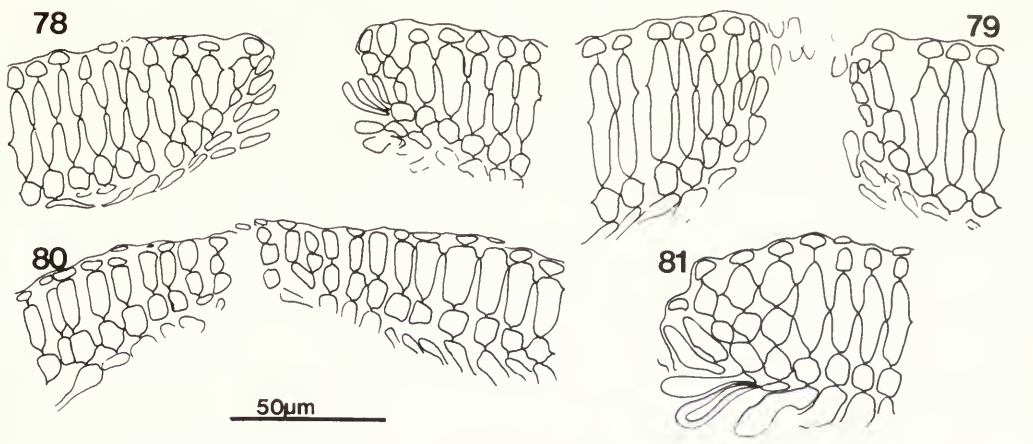
While the three-celled roof with a tall, relatively thin middle cell can be perceived throughout var. *pustulatum*, the actual height of the middle cell varies from the very tall ones seen in plants on a number of hosts in some Scottish localities (Fig. 79), to the medium- sized ones of 'typical' *Mastocarpus*/*Chondrus* epiphytes (Fig. 23), to the relatively short ones seen in occasional globose conceptacles (Fig. 80).

DISTRIBUTION. *British Isles*: From all parts of the British Isles where suitable plant hosts or other substrata occur, i.e. virtually throughout except for parts of the east coast south of Yorkshire. *World*: Confirmed only from the Faeroes, southern Norway, Helgoland, northern France (i.e. other European records examined have been confirmed as belonging to different species or varieties), South Africa and Southern Australia. The name has been used elsewhere but extra-European records need confirmation.



Figs 74–77 Scanning electron micrographs to show features of a thick plant of *Titanoderma pustulatum* var. *pustulatum* from Shetland Islands (86/130) (scales in μm).

74. Surface view of bisporangial plant showing the partially immersed conceptacles.
75. Surface view of the remaining roof surface of an immersed conceptacle.
76. Vertical fracture of a bisporangial plant showing the thick thallus and bisporangia in a conceptacle.
77. Roof surface of an old conceptacle showing calcified ridges and epithallial concavities with pit connections (arrow) to the subtending cell.



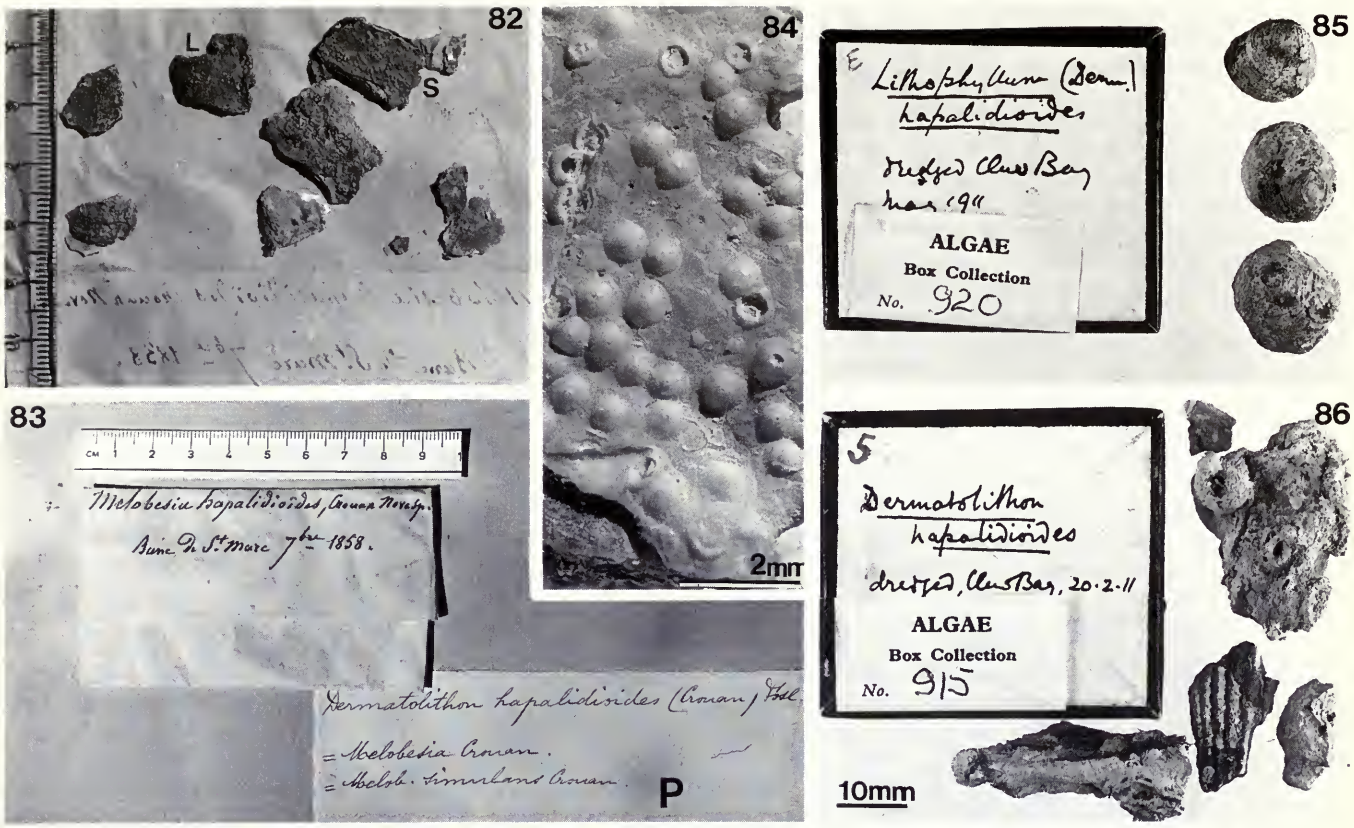
Figs 78–81 Vertical sections to show variation in roof structure of *Titanoderma pustulatum* var. *pustulatum*.
78. Average roof in plant growing on *Laminaria* stipe (85/27).
79. Very tall cells in plant growing on *Laminaria* blade (85/28).
80. Very short cells on plant growing on *Phyllophora crispa* (85/29).
81. Development of extra cells near the ostiole in lectotype specimen of *Lithophyllum pustulatum* f. *faeroense* (TRH) (cf. Fig. 60).

HABITAT AND PHENOLOGY. Var. *pustulatum* grows principally on red algae, most notably on *Chondrus crispus* and *Mastocarpus stellatus*, often it is superimposed on *Melobesia membranacea*, and it usually occurs in exposed rather than sheltered localities. Other hosts include *Palmaria palmata, Phyllophora crispa*, *P. pseudoceranoides* (S. Gmelin) Newroth & A. Taylor, *Gymnogongrus crenulatus* (Turner) J. Agardh, *Furcellaria lumbricalis, Cladostephus spongiosus* and *Laminaria* spp.—especially *L. hyperborea*. Epilithic, and rarely epizoic, plants of *T. pustulatum* have been found quite commonly in intertidal and subtidal situations but epiphytic plants probably occur mainly in the intertidal, although a few subtidal records have been confirmed. Records of fertile bisporangial plants have been confirmed for all seasons of the year, but prolific spore settlement has been observed only in summer (June-August).

HERBARIUM SPECIMENS CONFIRMED AS T. PUSTULATUM VAR. PUSTULATUM. As *Melobesia pustulata*, France, Cherbourg (on *Chondrus*), Kützing 1591, (L 940.317.499!); as *Choreonema laminariae*, Norway, Kristiansund, Foslie (BM!); as *Lithophyllum macrocarpum*, Faeroes, Bodring, paa *Gigartina mamillosa*, 18.15/11.97, H. Jønsson, F.Børgesen 284 (TRH!) (Fig. 81) [this specimen now selected as lectotype of f. *faeroensis*]; as *Dermatolithon polymorphum* [presumably in error for *pustulatum*], British Isles, Co. Mayo, Clare Island, south shore, 15 April 1909, on *Gigartina*, A. D. Cotton (BM-K!) [presumed to be the basis of the record of *D. pustulatum* in Lemoine, 1913*b*: 138]; as *Dermatolithon hapalidioides*, Faeroes, Kvanhauge, on *Patella*, 7 May 1896, F. Børgesen (C!); British Isles specimens in herb. *Chamberlain*: Yorkshire, Robin Hood's Bay, on *Mastocarpus stellatus*, intertidal, 5 September 1975, 75/143; Co. Wexford, Crossfintan, on *Chondrus crispus*, intertidal, 3 August 1977, 77/242; Devon, Beer, the Gully, on *C. crispus*, intertidal, 27 February 1976, 76/76; Cornwall, Penlee Point, on *C. crispus*, intertidal, 22 January 1981, 81/1; Northumberland, Berwick-upon-Tweed, on *C. crispus* and *M. stellatus*, intertidal, 11 February 1982, 82/1; Dorset, Lulworth, on *Laminaria digitata* with *Titanoderma laminariae*, 3–5 m depth, 15 March 1983, 83/225; Dyfed, West Angle, on *C. crispus*, intertidal, 18 February 1984, 84/59; Devon, Langerstone Point, on *C. crispus*, low tide channel, 4 March, 1984, 84/99; Isle of Man, Niarbyl, on *C. crispus*, intertidal, 18 March 1984, 84/146; Isle of Man, Port St Mary, on *Laminaria digitata*, upper subtidal, 19 March 1984, 84/150; Scilly Isles, St Agnes, on *C. crispus* and *M. stellatus*, intertidal, July 1984, 84/286; Mull, Gribun, on *Laminaria* stipe and blade, *Phyllophora crispa* and *Chondrus crispus*, intertidal, 7 March 1985, 85/27–30; Shetland Isles, South Mainland, on *Fucus serratus*, *C. crispus* and *M. stellatus*, intertidal, 13 August 1986, 86/129–130; Dorset, Lulworth, on *Laminaria* with *Titanoderma laminariae*, 1–2 m depth, 9 September 1986, 86/134; Jersey, Portelet Bay, on *C. crispus*, intertidal, October 1986, 86/147; Dorset, Kimmeridge, on rock, intertidal, 17 October 1986, 86/153; Devon, Wembury, on *C. crispus*, intertidal, 24 November 1988, 88/126.

HERBARIUM SPECIMENS MISIDENTIFIED AS T. PUSTULATUM VAR. PUSTULATUM. As *Melobesia pustulata*, Italy, Livorno, on '*Acanthatylo heredia*' (= *Phyllophora*), Kützing (L 940.317.500!) (= var. *macrocarpum*); Italy, M.mediterranea, ad *Sargassum linifolium* (L 940.317.501!) (= a mixture of species, mainly *Fosliella* spp. and var. *canellatum*); as *Melobesia pustulata* β *canellata*, Mediterranean, on *Cryptacantha squarrosa*, Kützing (L 940.317.502!) and *Ceramium rubrum*, Kützing (L 940.317.503!) (= var. *canellatum*); as *Dermatolithon pustulatum* f. *laminariae*, British Isles, Co. Mayo, Clare Is., on *Laminaria cloustonii*, April 1909, A. D. Cotton (BM-K!) (= *Phymatolithon* sp. and *Lithophyllum crouanii*); as *Lithophyllum pustulatum*, Sweden, Bohuslän, Kristineberg, on *Phyllophora*, 30 June 1949, Suneson (LD! and Suneson's personal collection!) (= var. *macrocarpum*).

1b. **Titanoderma pustulatum** var. **macrocarpum** (Rosanoff) Y. Chamberlain, **comb.nov.**— *Melobesia macrocarpa* Rosanoff in *Mem.Soc.imp.Sci.nat.Cherbourg* **12**: 74 (1866). —*Dermatolithon pustulatum* f. *macrocarpum* (Rosanoff) Foslie in *K.nor. Vidensk.Selsk.Skr.* **1898**(3): 11(1898).— *Lithophyllum macrocarpum* (Rosanoff) Foslie in *Wiss. Meeresunters. Helgol.* **7**(1): 9(1904).—*Lithophyllum pus-*



Figs 82–86 Type and other historically important specimens of *Titanoderma pustulatum* var.*macrocarpum*.
82–84. Type material of *Melobesia hapalidioides* (CO).
82. Opened packet containing lectotype (L) and isolectotype (S) used for examination.
83. Closed packet labelled by the Crouans; herbarium label (P) written by Picquenard.
84. Isolectotype showing abruptly conical conceptacles.
85–86. Specimens collected by A.D.Cotton during the Clare Island Survey and identified by Mme P.Lemoine as *Lithophyllum hapalidioides* (BM).

tulatum f. *macrocarpum* (Rosanoff) Foslie in *K.nor. Vidensk. Selsk.Skr.* **1905**(3): 117 (1905).—*Titanoderma macrocarpum* (Rosanoff) Y. Chamberlain in *Cryptogamie: Algol.* **7**: 203 (1986). Type: France, Cherbourg, Rochers des Flamands, on *Phyllophora rubens*, 19 March 1863, *Le Jolis*, Alg.mar. Cherbourg 276 (CHE!—lectotype; CHE!—isolectotypes). Figs 82–154.

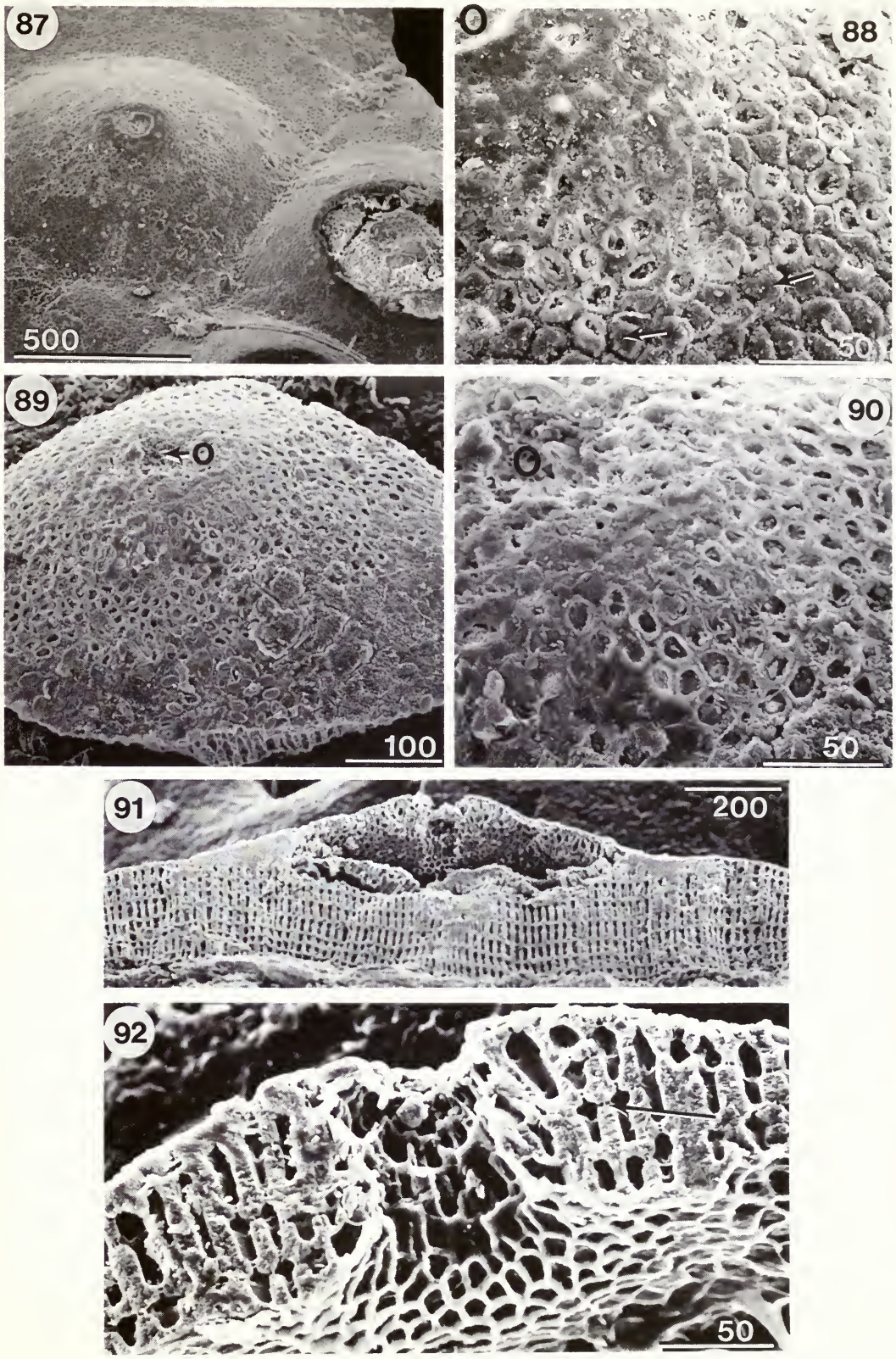
Melobesia simulans P. & H. Crouan, *Fl. Finistère*: 149 (1867). Type: France, dragué Rade de Brest, *P.-L. & H.-M. Crouan* (CO!—lectotype selected here; CO!—isolectotypes). (Fig. 108).

Melobesia hapalidioides P. & H. Crouan, *Fl. Finistère*: 150 (1867).—*Dermatolithon hapalidioides* Foslie in *K.nor. Vidensk.Selsk.Skr.* **1898**(3): 11 (1898).—*Lithophyllum hapalidioides* (P. & H. Crouan) Heydrich in *Bot.Jb.* **28**: 537 (1901);—*L. hapalidioides* (P. & H. Crouan) Foslie in *K.nor. Vidensk.Selsk.Skr.* **1905**(3): 128 (1905);—*Tenarea hapalidioides* (P. & H. Crouan) W. & P. Adey in *Br.phycol. J.* **8**: 394 (1973).—*Titanoderma hapalidioides* (P. & H. Crouan) J. Price, D. John & G. W. Lawson in *Bull.Br. Mus.nat.Hist.* (Bot.) **15**: 86 (1986). Type: France, Banc de St Marc, Septembre 1858, *P.-L. & H.-M. Crouan* (CO!—lectotype selected here; CO!—isolectotypes). (Figs 82, 83).

Lithothamnion adplicitum Foslie in *K.nor. Vidensk.Selsk.Skr.* **1897**(1): 17 (1897).—*Dermatolithon adplicitum* (Foslie) Foslie in *K.nor. Vidensk.Selsk.Skr.* **1905**(3): 128 (1905). Type: British Isles, Sussex, Bognor, on *Pholas* shells, October 1887, E. A. Batters (BM [Box 573]!—holotype). (Fig. 120).

ILLUSTRATIONS. As *Melobesia macrocarpa*, Rosanoff in *Mém.Soc.Imp.Sci.nat.Cherbourg* **12**: pl.IV, figs 4–6, 8, 11-20 (1866); as *Titanoderma macrocarpum*, Y. Chamberlain in *Cryptogamie: Algol,* **7**: figs 12–21 (1986); as *Lithophyllum pustulatum*, Suneson in *Acta Univ.lund.* II, **33**: figs 22, 23, pl.VIII, fig.37 (1943).

DESCRIPTION. Plants mainly epilithic, more rarely epiphytic or epizoic, flat, closely adherent or becoming extensively imbricating, to *c.* 50 mm diameter, 700 μm thick, tapering to a bistratose margin, rose- to salmon- to red- to orange-pink, somewhat satiny, surface smooth. Single layer of *axial filaments* with cells mainly obliquely orientated, but often with areas of short vertically orientated cells, cells 5–139 μm high × 9–36 μm diameter, *erect filaments* absent or to 16 cells long, cells 5–80 μm long × 9–41 μm diameter, often with particularly pronounced secondary pit connections, *epithallial cells* flattened, thallus cell cytoplasmic contents usually sparse but lower cells frequently full of large (to 6 μm diameter) starch grains, new axial filaments often regenerating from cells of erect filaments, trichocytes rare. *Gametangial and tetsasporangial* plants not seen; *bisporangial conceptacles*



Figs 87–92 Scanning electron micrographs of isolectotype specimen of *Melobesia hapalidioides* (CO) (scales in μm).

87. Mature conceptacles.
88. Roof of mature conceptacle immediately below ostiole (o) showing bulbously calcified roof cells (arrow).
89. Old conceptacle with ostiole (o).
90. Detail of roof surface of old conceptacle below the ostiole (o), the bulbous calcification has worn away.
91. Vertical fracture of thallus and conceptacle showing the strongly aligned thallus cells.
92. Vertical fracture of ostiole. Note the tube-like secondary pit connections between roof cells (arrow).

widely spaced to densely crowded, somewhat domed to hemispherical, sometimes arising gradually from thallus surface but usually well defined at conceptacle base, 400–900 μm external diameter, conceptacle surface with horseshoe-like to more or less stepped calcification, conceptacle chamber low elliptical to hemispherical, 150–540 μm diameter, 65–210 μm high, roof 52–104 μm thick, roof thickening to 3–7 cell layers near ostiole with cells more or less isodiametric, sometimes with papillae lining the ostiole, columella slightly- to well-developed, up to *c.*80 bisporangia, 50–117 μm long × 21–65 μm diameter, old conceptacles often becoming buried in thallus.

[Imbricating plants, lacking erect filaments, are described under variation range, see p.00.]

HISTORICAL. Rosanoff (1866) described *Melobesia macrocarpa* on the basis of plants growing on *Phyllophora* at Cherbourg (Le Jolis, Mar.Alg.Cherbourg, 276, CHE!), and this species was lectotypified by Chamberlain (1986, as *Titanoderma macrocarpum*) and the lectotype specimen described in further detail. Suneson's (1943—as *Lithophyllum pustulatum*) epiphytic Swedish plants are very similar to the type material. The Crouan brothers (1867) described *Melobesia hapalidioides* on the basis of plants growing on 'coquilles d'Anomie' on the Banc de St Marc in the area of Brest in western France (Figs 82–84). At the same time they described *M. simulans* which, as the name implies, they considered similar to *M. hapalidioides*, the principal differences mentioned being the presence of bisporangia in the pink *M. hapalidioides* and tetrasporangia in the reddish pink *M. simulans*.

Foslie (1898*b*) first mentioned *M. hapalidioides* when he listed it in his newly erected genus *Dermatolithon*; later (Foslie, 1900*a*) he described some Crouan specimens of *Melobesia* in PC and concluded that *M. hapalidioides* and *M. simulans* were conspecific. Subsequent authors (e.g. Hamel & Lemoine, 1953) have accepted this conclusion. Foslie (1905*a*) discussed *M. hapalidioides* extensively in *Northern Lithothamnia*, and he transferred it to *Lithophyllum*, apparently without knowing that Heydrich (1901) had made the same transfer, although without quoting the basionym and thus invalidating the recombination. Foslie commented that he had difficulty in distinguishing between *L. hapalidioides* (Foslie, 1905*a*: 123) and *L. macrocarpum* (Foslie, 1905*a*: 129) but nevertheless retained the former as a distinct species, perhaps on the basis that it was epilithic or epizoic rather than epiphytic. Subsequently Foslie compared *L. hapalidioides* with various other species of *Titanoderma* (as *Lithophyllum*) (Foslie, 1905*c*, 1907*a*, 1908); finally he transferred the species back again to *Dermatolithon* (Foslie, 1909: 58).

Lemoine recorded *T. pustulatum* var. *macrocarpum* (as *Lithophyllum hapalidioides)* many times and apparently regarded it mainly as an epilithic/epizoic species although, like Foslie, she retained the partially epiphytic *confinis* as a variety. Lemoine (1913*b*) first recorded *Lithophyllum (Dermatolithon) hapalidioides* from the west coast of Ireland (BM! see Figs 85, 86). She stated that it was similar to *L. pustulatum*, but the latter had pores in its cells; its cell 'rangées' (i.e. horizontal rows) were separated by strongly-staining membranes; and its cells attained greater maximum size. Lemoine (1923*a*) later recorded *L. hapalidioides* as forming thin pink thalli growing on rocks on Rockall. Unfortunately the specimen (PC!) is too small to identify but it may be var. *confine*, a plant recently collected on Rockall (see p. 60). Lemoine (1923*b*) also recorded *L. hapalidioides* from the subtidal in La Manche (English Channel). She found the species to be very variable, sometimes the thalli were regularly orbicular (e.g. Lemoine, 1913*b*) but at other times, such as in the subtidal specimens from Ile Tenedos (now Bozcaada) off the north-east Aegean coast of Turkey (Lemoine, 1915: 18, PC!) she found both more or less orbicular, quite thick plants, and plants comprising superimposing layers of thalli lacking erect filaments, with cells of axial filaments sometimes vertical and sometimes oblique. She also recorded this growth form (Lemoine, 1931) from the Ile Cézembre in western France. It has not been possible to find this material, but other material from the Pointe de Cancaval (PC!) in the same area, and mentioned in the same paper, has been examined and is the imbricating growth form. In her key Lemoine (1971: 551) referred otherwise to var. *macrocarpa* (as *hapalidioides*) as having erect filaments up to 10 cells long and a sterile margin from 14–26 cells wide. Dawson (1955) keyed out var. *macrocarpum* (as *Dermatolithon hapalidioides*) as growing on 'stones, pebbles and mollusk shells', with a thallus up to 300 μm thick and tetrasporangial conceptacles 220–400 μm diameter.

Lemoine (1915, 1921, 1924, 1927, 1957) recorded *T. pustulatum* var. *macrocarpum* (as *Lithophyllum hapalidioides)* from a number of Mediterranean localities. Other Mediterranean records have been published by Lewalle (1961—Naples), Cormaci & Furnari (1979—eastern Sicily), and Boudouresque & Perret (1977—Corsica). Bressan (1974) recorded *Dermatolithon hapalidioides* f. *typica* as being common on shells and worm tubes throughout Italy and Lewalle's (1961) material was growing on a stone. In one paper (Battiato et al, 1982—Ischia, Naples) however, the species is recorded as growing on *Posidonia*. Although none of the Mediterranean records has been confirmed, it seems probable that var. *macrocarpum* occurs commonly throughout the Mediterranean, Adriatic (Foslie, 1909: 48), and Aegean Seas (Lemoine, 1915), particularly growing on shells and stones. Lemoine's (1929) record from the Canary Islands (C!) of *L. hapalidioides* also pertains to var. *macrocarpum*.

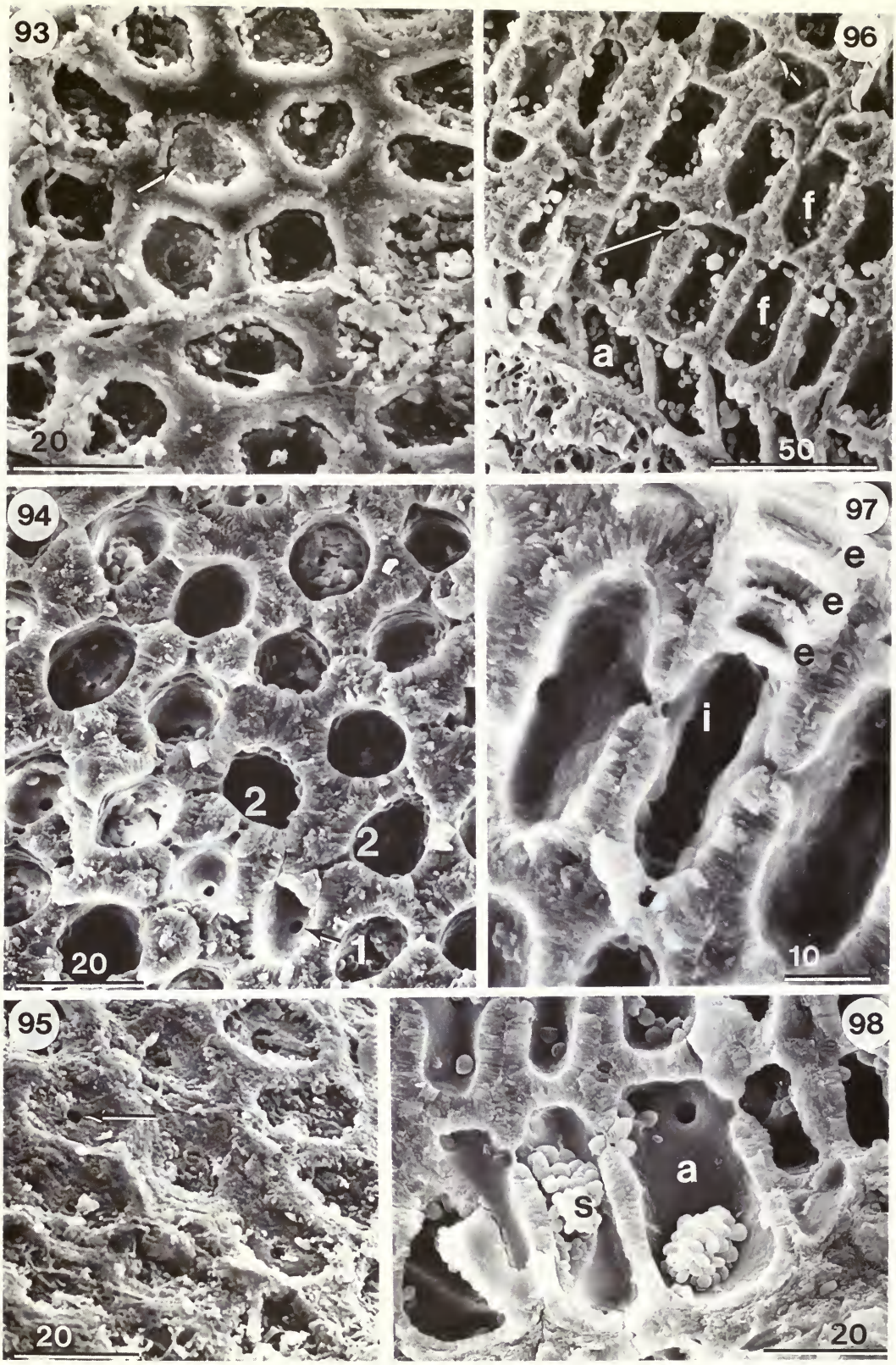
Adey & Adey (1973) retained *Tenarea hapalidioides* (now var. *macrocarpum*) and *T. confinis* as distinct species. They segregated the species on the basis of colour, cell size and conceptacle size differences, but did not examine conceptacle roof differences. One of their '*T. hapalidioides*' specimens (USNC! 70–4–17, Wembury) is epilithic material of var. *pustulatum* with a three-celled roof structure, but most of their material pertains to var. *macrocarpum*.

The imbricating growth form of var. *macrocarpum* has not been characterized before but some particularly extensive specimens growing on shells were collected by Batters at Bognor (Fig. 120) together with the type of *Lithothamnion adplicitum* Foslie (now var. *macrocarpum*). Batters also collected this growth form at Plymouth (BM Box 573!), identifying the plant as *Lithothamnion strømfeltii* f. *tenuissima*. A note on the specimen by Foslie concludes that this is a misidentification and suggests *L. adplicitum* as one of several alternative names.

NOTES ON TYPE SPECIMENS.

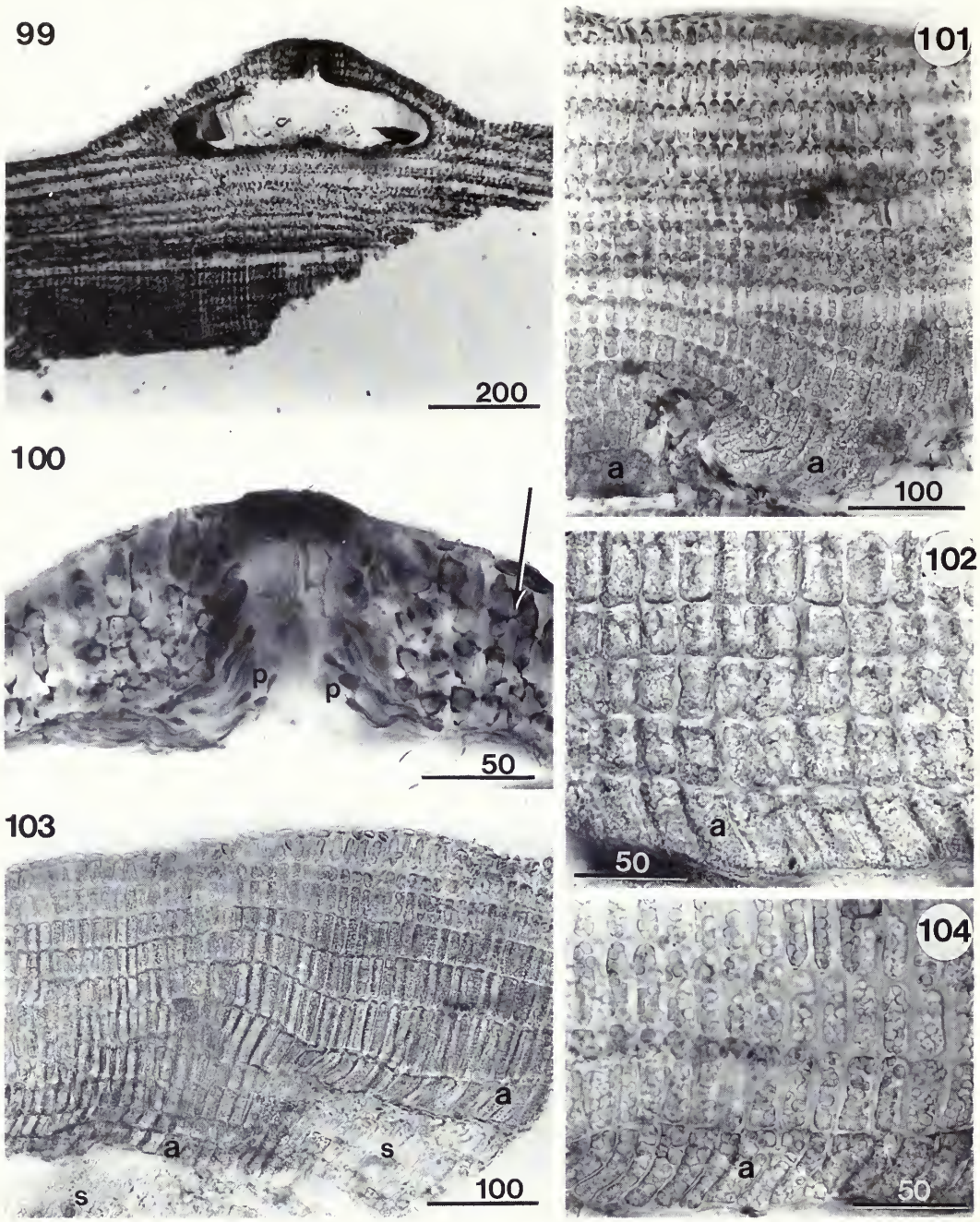
(1). *Melobesia macrocarpa* Rosanoff. This taxon is lectotypified and the epiphytic lectotype described in detail in Chamberlain (1986).

(2). *Melobesia hapalidioides* P. & H. Crouan (1867: 150). Lectotype (now designated): France, Banc de St Marc,



Figs 93–98 Scanning electron micrographs to show thallus features of the lectotype specimen of *Melobesia hapalidioides* (scales in μm).

93. Thallus surface showing calcified ridges encircling epithallial concavities (arrow) in which epithallial cells remain.
94. Horizontal fracture through thallus cells with heavily calcified cell walls, primary pit connections (1) and tube-like secondary pit connections (2).
95. Old thallus surface with epithallial concavities and central holes (arrow) marking the position of the primary pit connections.
96. Vertical fracture of erect filament cells (f) in aligned horizontal rows with secondary pit connections (arrows) high in the cells, and short oblique axial cells (a).
97. Vertical fracture of subepithallial initial (i) and tier of epithallial cells (e), the uppermost of which is probably being shed.
98. Vertical fracture of axial cells (a) containing starch grains (S).



Figs 99–104 Vertical sections of *Titanoderma pustulatum* var. *macrocarpum* (scales in μm).
99–102. Isolectotype of *Melobesia hapalidioides* (CO)
99. Bisporangial conceptacle borne on a thallus with aligned perithallial cells.
100. Ostiole showing small papillae (p) lining the canal and roof cells with tube-like secondary pit connections (arrow).
101. Thallus showing upper, aligned erect filament cells, and axial (a) and lower erect filament cells packed with floridean starch grains.
102. Axial (a) and lower erect filament cells with immature starch grains.
103. Thallus (84/158) growing on maerl in Ireland. New axial filaments (a) have regenerated above senescent thallus (s).
104. Axial (a) and lower erect filament cells full of large starch grains (84/179).

Septembre 1858, P.-L. & H.-M. Crouan (CO!). (Figs 82, 83).

Four packets of *Melobesia hapalidioides* are present in the Crouans' herbarium at Concarneau and the above lectotype (Figs 82, 83) was chosen because that locality was specified in the protologue (Crouan & Crouan, 1867). The packet (Fig. 82) contains nine fragments of shell bearing rose- to mauve-pink plants with prominent, conical conceptacles and thalli that are quite thick centrally but taper to the margin. The remaining eight plants can be regarded as isolectotypes.

Thallus cells of the lectotype were observed under the SEM (Figs 8, 93–98). The axial cells vary from being short and

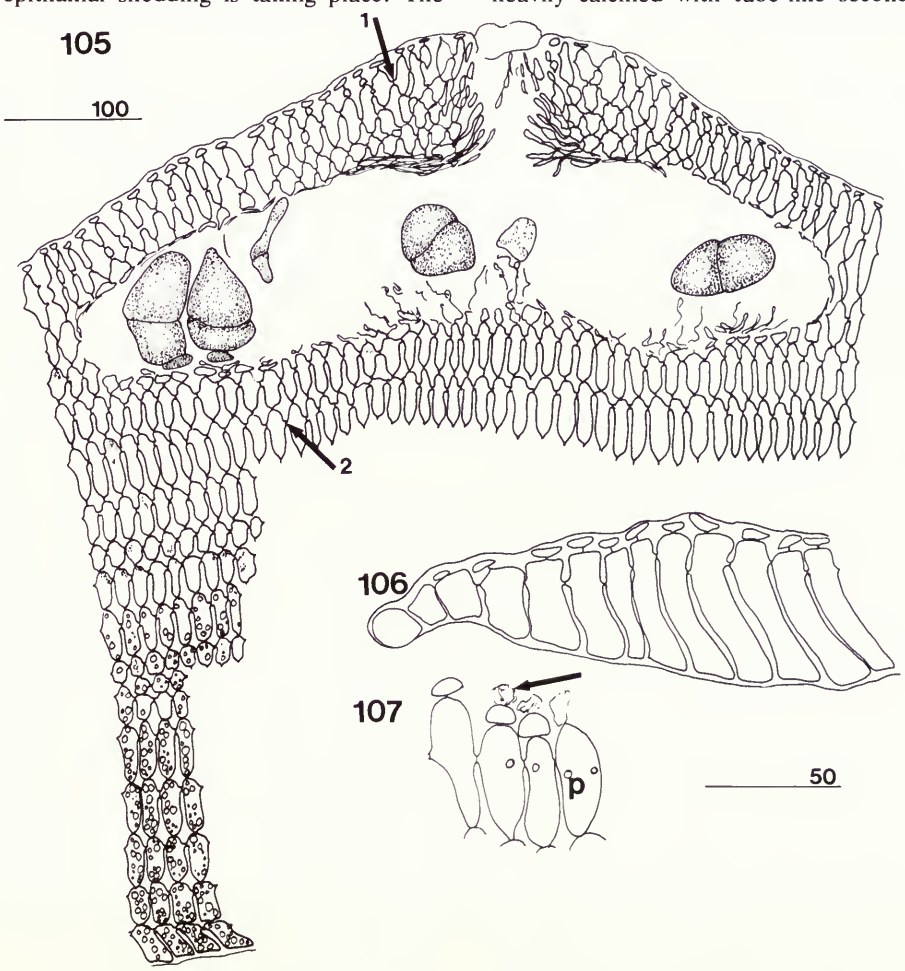
trapezoid (Fig. 96) to about twice as tall as wide (Fig. 98). Cells of erect filaments (Figs 8, 96) are more or less isodiametric to about twice as long as wide. They have heavily calcified side walls and both they and the axial cells contain abundant starch grains. Tube-like secondary pit connections occur frequently between contiguous cells of erect filaments (Figs 8, 94, 96), usually situated about two thirds of the way up the cells. Subepithallial initials (Fig. 97) are elongated and flattened epithallial cells (Fig. 97) may occur up to three cells deep.

In surface view (Figs 93, 95) the lectotype shows a honeycomb-like structure with calcified ridges surrounding remnants of epithallial cells (Fig. 93), or epithallial concavities (Fig. 95) in which pit connections mark the points where epithallial cells had been attached.

Conical bisporangial conceptacles (Fig. 45) appear distinctly delimited from the thallus surface at their periphery. They have horseshoe-like calcification of roof cells (Fig. 46), each cell having a small hole presumably where an epithallial cell had been attached. Lower down the conceptacle, the cells are either honeycomb-like, or show a structure (Fig. 47) similar to that seen in British Isles plants of var. *macrocarpum* (Figs 30, 31) in which epithallial shedding is taking place. The conceptacle chamber measures *c.*350 μm diameter × 125 μm high and the roof measures *c.*70 μm thick.

An isolectotype plant (Fig. 82, at letter S) has a bistratose thallus margin (Fig. 106) and oblique axial cells (Figs 101, 102, 105) measuring 14–90 μm high × 9–19 μm diameter. Lower thallus cells contain large starch grains. Erect filaments are up to 16 cells long (Figs 99, 101, 102, 105) and their cells measure 20–33 μm long × 9–17 μm diameter. Contiguous cells occur in horizontally aligned rows (Figs 91, 102, 105) and the cells are joined by secondary pit connections about two thirds of the way up the cell.

Bisporangial conceptacles of the isolectotype (Figs 84, 87, 89) are broadly conical and distinctly delimited from the thallus surface. Conceptacle surfaces show bulbous calcification (Fig. 88) which becomes honeycomb-like (Fig. 90) as the conceptacles age. Conceptacles measure up to 900 μm external diameter. In vertical fracture (Fig. 91) and vertical section (Figs 99, 105) the conceptacle chamber is broadly elliptical, measuring *c.*600 μm diameter × 125 μm high, the roof measuring *c.*100 μm thick. The conceptacle roof (Fig. 105) is two to three cells thick peripherally thickening to five cells thick at the ostiole (Figs 99, 105). Roof cells (Fig. 92) are heavily calcified with tube-like secondary pit connections;

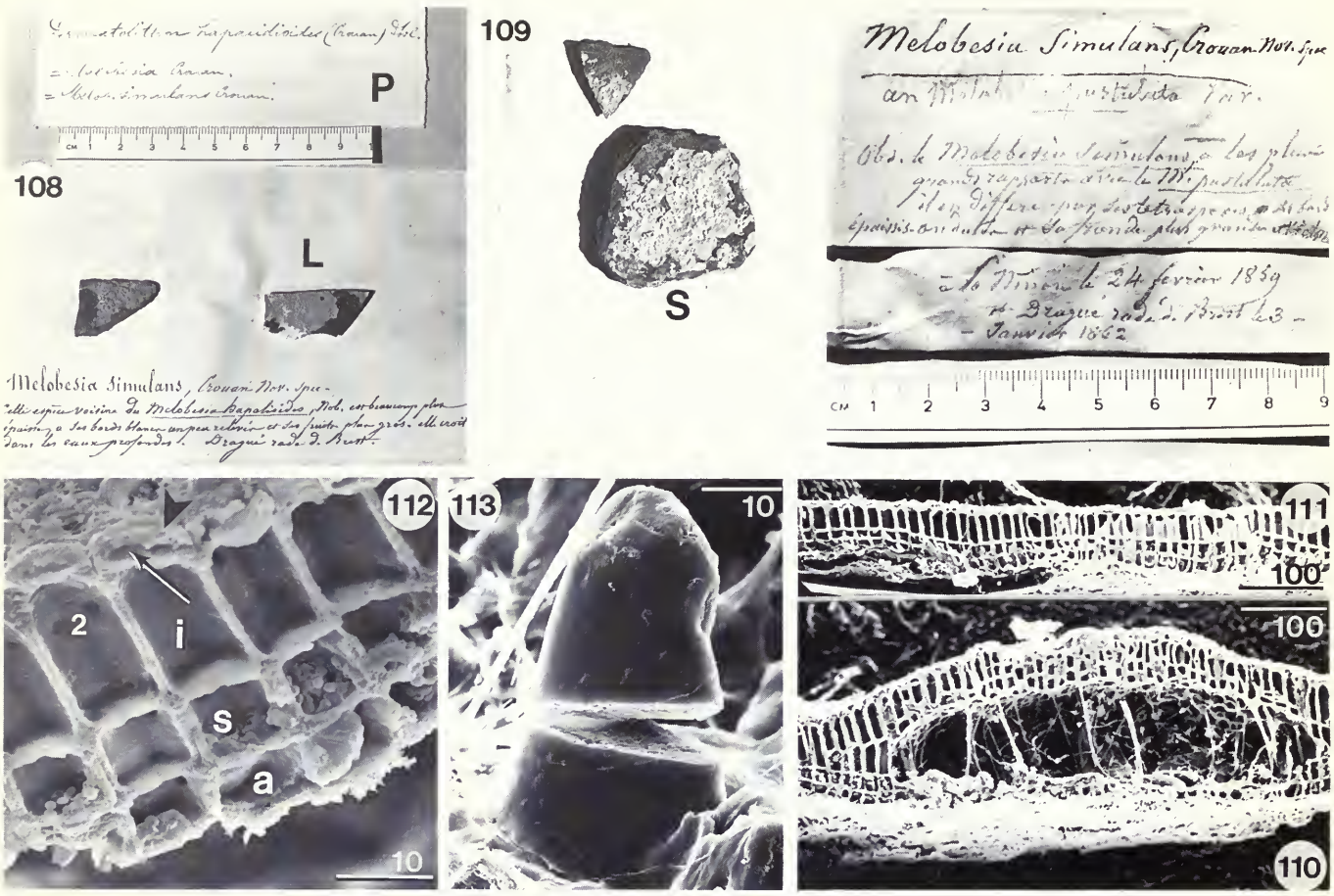


Figs 105–107 Vertical sections of *Titanoderma pustulatum* var. *macrocarpum* (scales in μm).

105. Bisporangial conceptacle and representative thallus cells of the isolectotype specimen (CO, see Figs 82–84) of *Melobesia hapalidioides*. Tube-like secondary pit connections occur between roof cells (1) and erect filament cells (2); the lower thallus cells contain starch grains.

106. Bistratose thallus margin (83/233).

107. Subepithallial cells of the thallus of the lectotype of *M. hapalidioides* showing old epithallial cells being shed from the thallus surface (arrow). Secondary pit connections (P) are seen in the initials.



Figs 108–113 Type material of *Melobesia simulans* (scales in μm in Figs 110–113).

108. Lectotype (L) of *Melobesia simulans* (CO), with label written by the Crouans. The herbarium label is in Picquenard's hand (P).
109. Isolectotype (S) of *M.simulans* (CO). The label on the packet is written by the Crouans.
110. Vertical fracture of conceptacle from the isolectotype
111–112. Vertical fracture of the thallus of the isolectotype, in 112 note the short axial cell (a) and tall subepithallial initial (i) showing secondary pit connections (2). The epithallial cell (arrow) is very short and can be related to its flat-topped surface view (arrowhead). Starch grains (s) are present.
113. Bisporangium from the isolectotype.

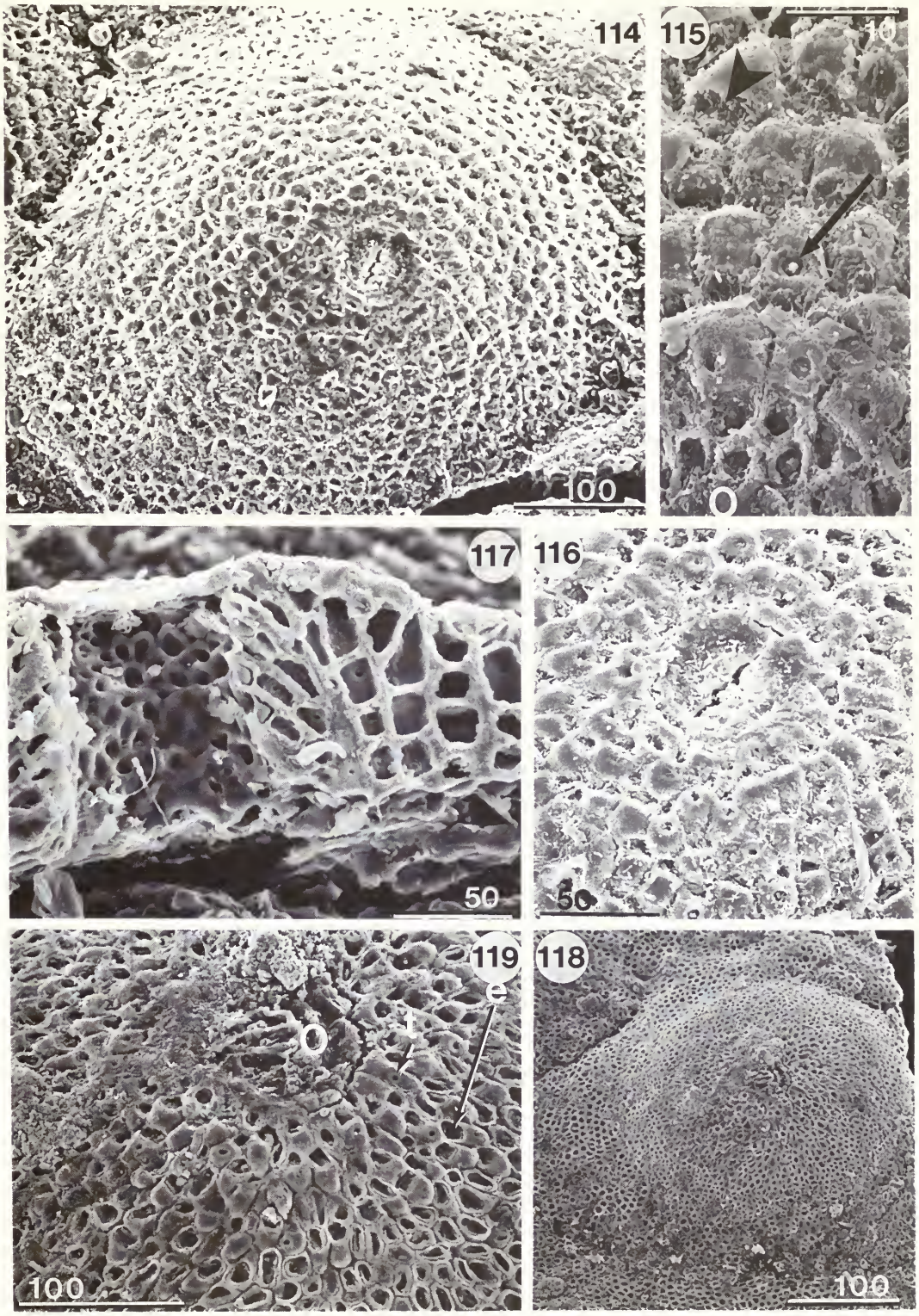
small papillae line the ostiole canal (Fig. 105). A small columella occurs centrally (Fig. 105) and 40 or more bisporangia are borne peripherally, measuring 52–72 μm long × 21–33 μm diameter.

(3). *Melobesia simulans* P. & H. Crouan (1867: 150). Lectotype (now designated): France, dragué, Rade de Brest, P.-L. and H.-M.Crouan (CO!) (Fig. 108).

There are two collections labelled *Melobesia simulans* (Figs 108, 109) in the Crouans' herbarium at Concarneau. One sample (Fig. 108) was collected by dredging in the Rade de Brest, the locality cited by the Crouans (1867). It comprises a fragment of porcelain and one of slate, and on the slate is a pink crustose plant with raised conceptacles which is now designated the lectotype. On the other fragment (Fig. 109) there is one, principal lobed plant with hemispherical conceptacles that are larger than the lectotype but similar in construction: this can be regarded as an isolectotype.

The thallus of the lectotype of *M. simulans* (Fig. 108) measures up to 210 μm thick. It is composed of axial filaments with cells measuring 18–47 μm high × 13–18 μm long and erect filaments up to three cells long (Fig. 143) with cells measuring 13–47 μm long × 8–19 μm diameter; the epithallial cells are flattened and lower thallus cells contain floridean starch grains. As the Crouans comment on the label, the plants appear thick; examination shows, however, that they are quite thin and there is evidence of imbrication occurring beneath the conceptacle (Fig. 142). A hemispherical conceptacle (Fig. 114) measures *c.*450 μm external diameter and the roof surface (Fig. 115) is composed of stepped, calcified cells cradling epithallial cells, trichocytes occur frequently. A sectioned conceptacle (Fig. 142) measures 390 μm internal diameter × 130 μm high, the roof is 90 μm thick and the roof filaments round the ostiole are composed of up to six cells including the epithallial cell. Bisporangia are borne peripherally.

The thallus of the isolectotype (Figs 111, 112) is also thin, composed of axial filaments with short cells, and two-celled erect filaments with tall subepithallial initials and short lower cells. The conceptacles (Fig. 110) measure up to 700 μm external diameter with a stepped surface as in the lectotype. In VS the conceptacle roof (Fig. 117) is 90 μm thick and is composed of filaments up to five cells long including the



Figs 114–119 Scanning electron micrographs of historically important specimens of *Titanoderma pustulatum* var. *macrocarpum* (scales in μm).

114–117. Lectotype specimen of *Melobesia simulans* (CO).

114. Bisporangial conceptacle.

115. Roof cells immediately below ostiole (o). Trichocytes (arrow) and epithallial concavities (arrowhead) are present.

116. Ostiole and stepped roof surface.

117. VS of ostiole of isolectotype of *Melobesia simulans* (CO), showing long roof filaments.

118–119. *Lithophyllum pustulatum* auct. Suneson, from Kristineberg, Sweden showing a conceptacle (118) and detail (119) of the stepped cells of the roof surrounding the ostiole (o). Epithallial concavities (e) are unusually large and trichocytes (t) occur.

epithallial cell; small papillae line the ostiole canal. Bisporangia (Fig. 113) are present.

The thin, imbricating thallus and the size and structure of the conceptacles of these plants resemble the imbricating growth form of var. *macrocarpum*, but they differ in showing some development of erect filaments.

(4). *Lithothamnion adplicitum* Foslie (1897: 17). Holotype: British Isles, Sussex, Bognor, on *Pholas* shells, October 1887, *E. A. Batters* (BM Box 573!) (Fig. 120).

The holotype of *Lithothamnion adplicitum* (Fig. 120), designated by Foslie (1897), comprises a single plant of about 30 mm diameter and up to 800 μm thick which has a lumpy, uneven surface and a non-fertile margin about 10 mm wide. Densely crowded conceptacles occur in the centre (Fig. 121) which vary from being domed (Figs 122, 125) to nearly immersed and measure up to 950 μm external diameter. The conceptacle roof has bulbous cells surrounding the ostiole (Fig. 123), while towards the base more or less hexagonal, flattened cell roofs occur (Fig. 124), having central small holes, presumably where epithallial cells have been shed.

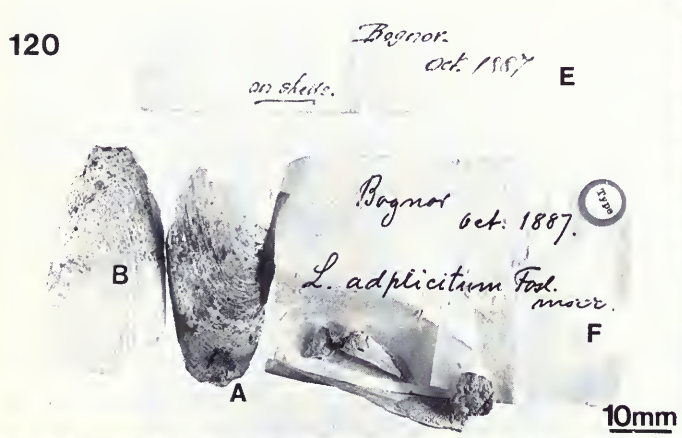
In VS (Fig. 126) the thallus is composed of more or less obliquely orientated axial cells (Fig. 128) measuring 13–25 μm long × 10–54 μm high. Erect filaments are up to 18 cells long; contiguous cells are noticeably aligned (Fig. 127) and the cells measure 13–67 μm long × 10–23 μm diameter. The upper thallus cells (Fig. 127) have sparse contents but floridean starch grains are abundant in lower cells (Fig. 128).

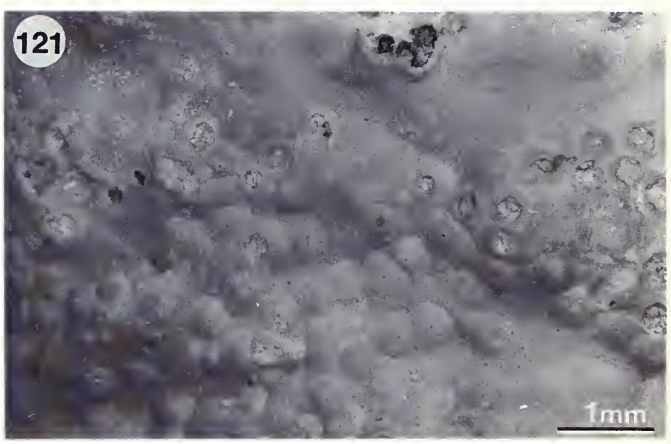
In VS (Figs 125, 145) the conceptacle has a broad, fairly shallow chamber measuring *c.*540 μm internal diameter × 130 μm high, the roof is *c.*95 μm thick; roof filaments are up to six cells long including the epithallial cell and the secondary pit connections are somewhat tube-like. Only shrivelled sporangia survive and there are remnants of a columella in the centre of the conceptacle floor. Old conceptacles (Fig. 146) mainly become buried in the thallus; many broken topped conceptacles are present on the thallus surface, but this seems to be due to damage.

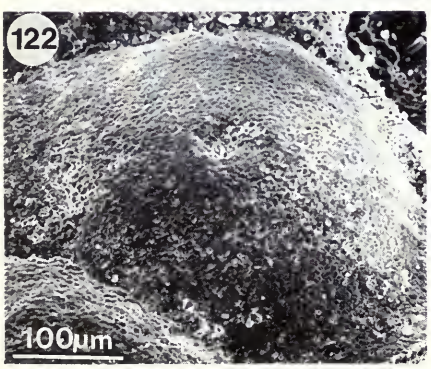
(5). Imbricating plants growing on the same *Pholas* shell as the holotype of *Lithothamnion adplicitum* (no. 4 above) (Fig. 120).

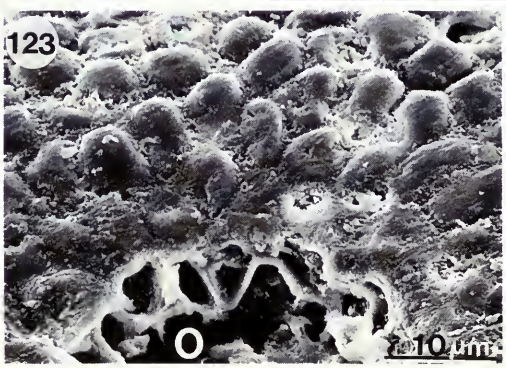
Plants of this growth form lack erect filaments. Similar plants have been found during this investigation and are described under variation range (see p. 48 [4]).

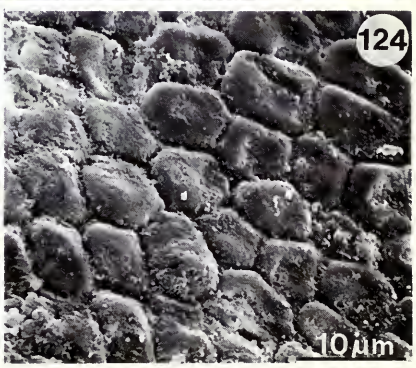
PLANT APPEARANCE. Epilithic and epizoic plants vary from orange-pink, to reddish to mauvish and plants of different colours may grow side by side; the orangish/reddish shades have come to be regarded as typical of var. *macrocarpum* (e.g. Hamel & Lemoine, 1953; Adey & Adey, 1973—both as *hapalidioides*). Epiphytic plants are rose-pink. Thalli growing on stones, shells, dead maerl, etc. (Figs 121, 137) are usually adherent, flat, and have a smooth, slightly glossy surface. They have a more or less extensive bistratose margin and





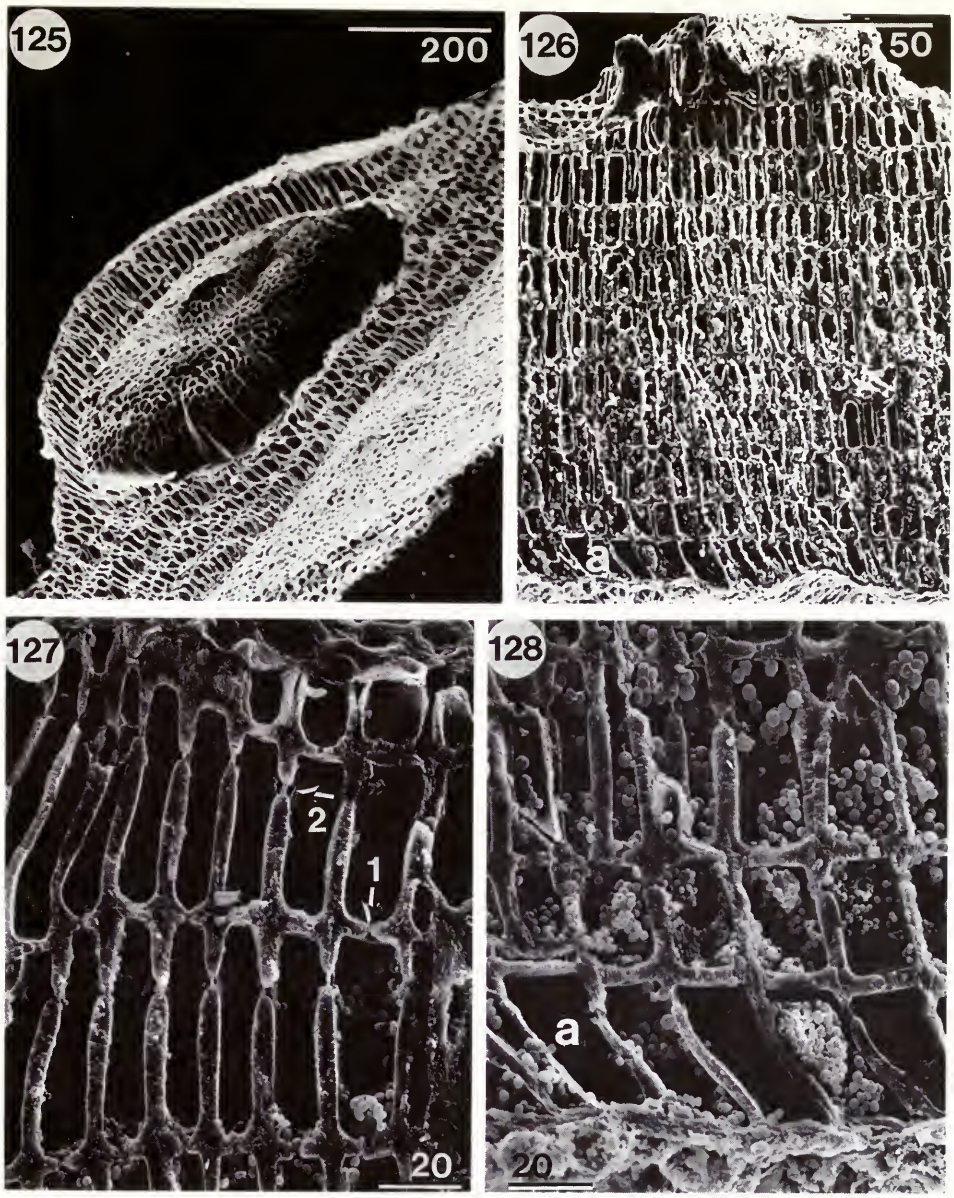






Figs 120–124 Holotype specimen of *Lithothamnion adplicitum* (BM) (scales in μm).

120. Holotype specimen (A) as specified in Foslie's description. Plant B pertains to the imbricating growth form of *Titanoderma pustulatum* var.*macrocarpum*. The labels are written by E. Batters (E) and M. Foslie (F).
121. Detail of A showing the crowded, somewhat raised conceptacles.
122. Bisporangial conceptacle.
123. Bulbously calcified conceptacle roof cells immediately below the ostiole (o).
124. Flattened epithallial cells at conceptacle base.



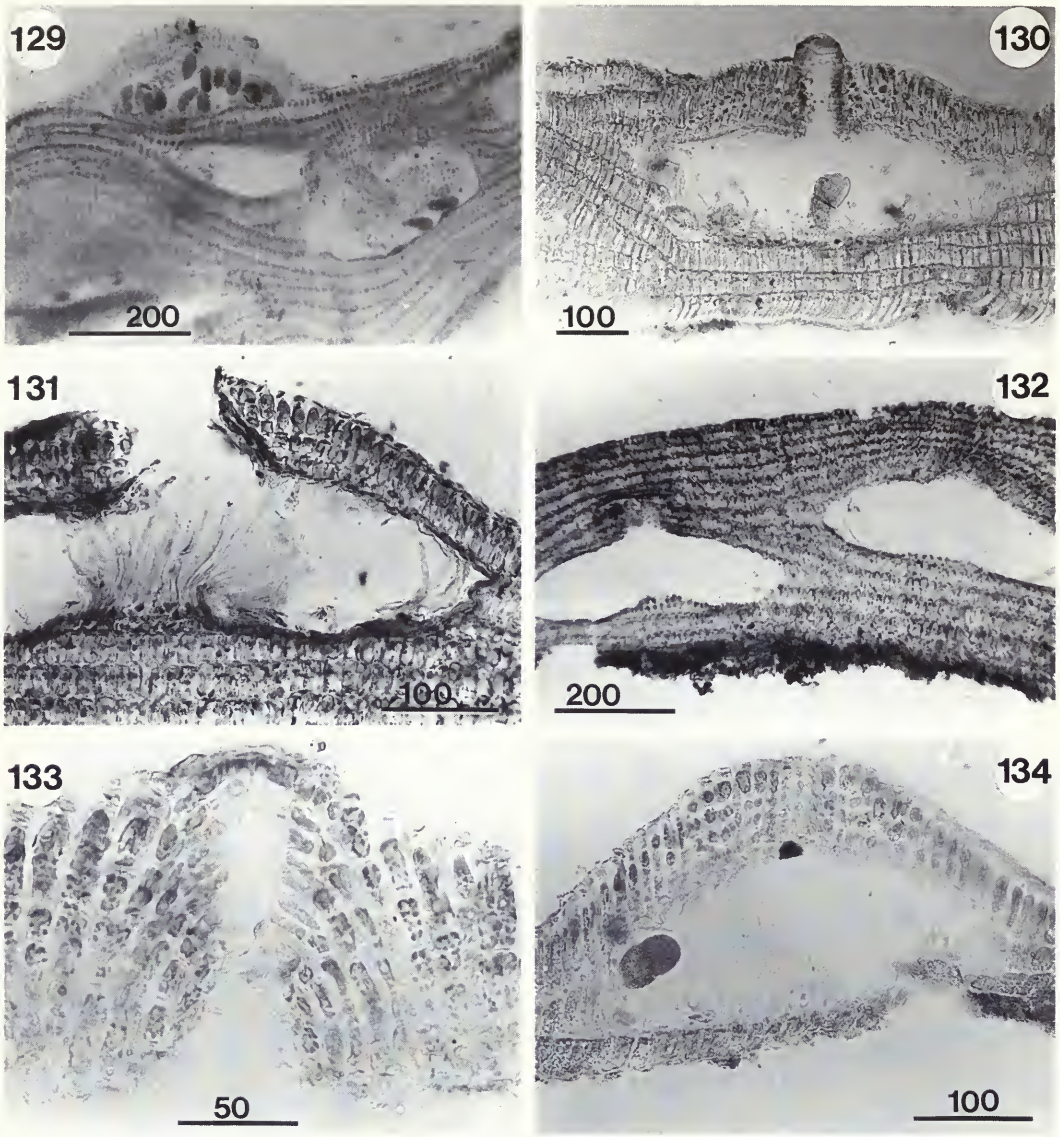
Figs 125–128 Holotype specimen of *Lithothamnion adplicitum* (BM) (scales in μm).

125. Bisporangial conceptacle.
126. Vertical fracture of thallus showing horizontally aligned erect filament cells and oblique axial cells (a).
127. Upper thallus cells showing primary (1) and secondary (2) pit connections and fairly light calcification.
128. Axial (a) and lower erect filament cells which both contain floridean starch grains.

thicken centrally; older plants frequently regenerate to form flaky, lobed growths overlying senescent remnants of the original plants. Often only scraps of thallus remain attached to the shells, stones, and algae among which they are growing. Sometimes, as in the lectotype of *Melobesia simulans* (Fig. 142), apparently thick, smooth plants prove to be quite tenuous and to have imbricating lobes beneath the surface. Epiphytic plants are usually flat, smooth, and non-imbricating (Chamberlain, 1986).

In surface view, bistratose thallus margins (Fig. 140) comprise radiating axial filaments with elongated cells and short epithallial concavities. Older thallus areas may show flat topped epithallial cells with small, central holes or protuberances (Figs 30–33) (see p. 21) or honeycomb-like ridges surrounding epithallial concavities (Fig. 139).

Bisporangial conceptacles occur singly, or in dense, appressed clusters (Figs 54, 121, 135, 137); they are usually more or less abruptly emergent, varying in shape from low-conical (Fig. 48) to domed (Figs 122, 135). Sometimes a small collar (Fig. 136) develops round the ostiole and a superimposed dome (Fig. 138) may occur. They are self-coloured when young and pale or white when old. The conceptacle surface is variable in structure; bulbous cells may occur in younger parts near the ostiole (Figs 123, 136), whereas mature roofs may have stepped cells (Fig. 138) or flat topped ones like those of the thallus (Fig. 124), trichocytes may occur in roof cells (Fig.



Figs 129–134 Vertical sections of bisporangial conceptacles of British Isles plants pertaining to *Titanoderma pustulatum* var. *macrocarpum* (scales in μm).

129. Plant with mature conceptacle growing on maerl (84/158) showing how the thallus weaves round obstructions in the substratum and old conceptacles become immersed.

130. Conceptacle with a slight funnel at the ostiole (84/311).

131 & 132. *Adey* 70–6–B, collected off the Isle of Wight. This material closely resembles *Lithothamnion adplicitum*, it has a somewhat thinner roof (Fig. 131), but a similar thallus (Fig. 132) with buried conceptacles.

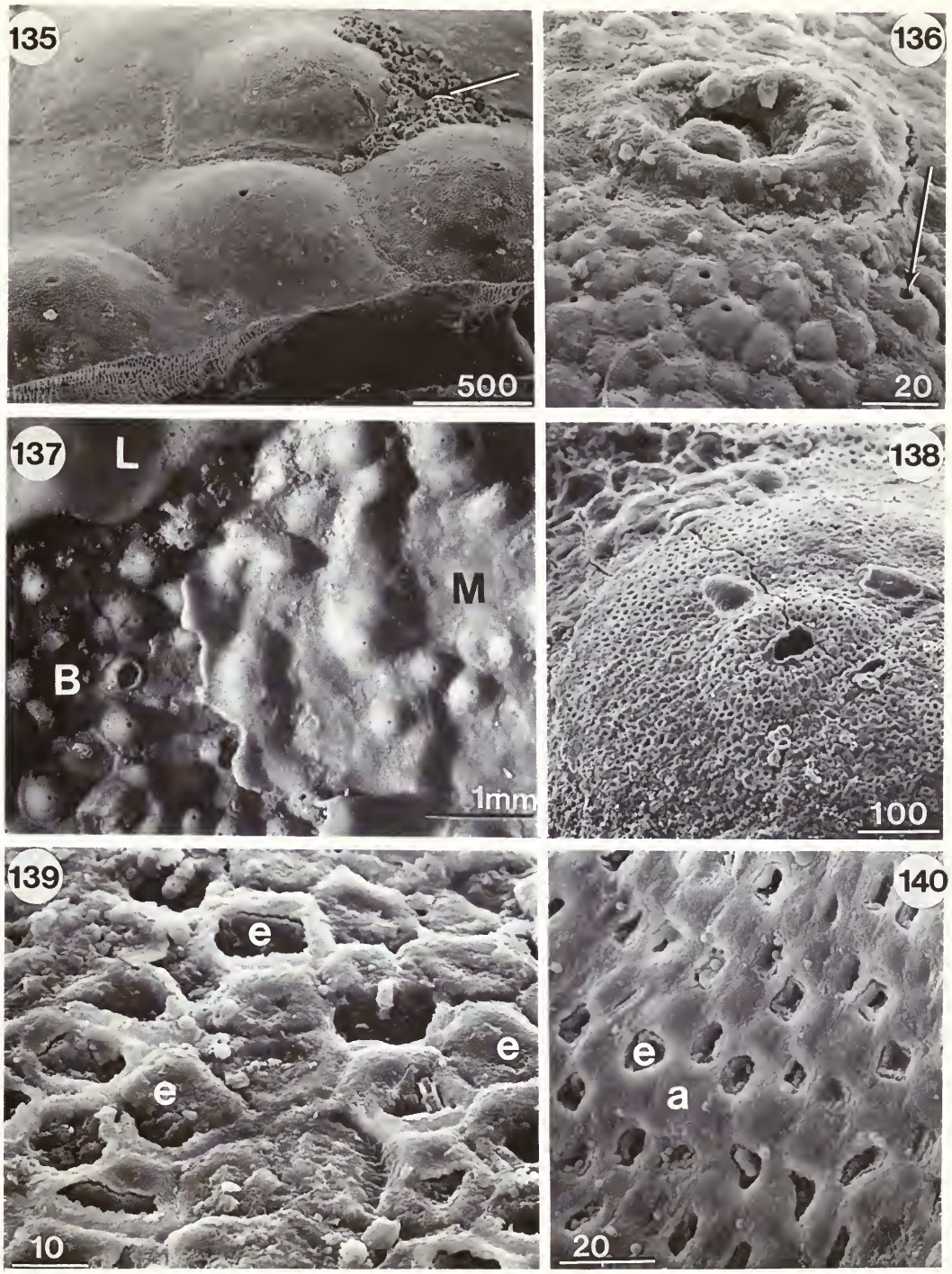
133. Ostiole canal surrounded by long roof filaments (83/72).

134. Plant of imbricating growth form from Dorset (86/135) composed of vertically orientated roof filaments and axial filaments which lack erect filaments

136). Some historical specimens have stepped roofs (Figs 115, 119), but the horseshoe-like calcification (Fig. 46), seen in the lectotype of *Melobesia hapalidioides*, has not been observed in the limited number of British Isles plants that have been examined under the SEM. It is possible that more extensive examination will elucidate the features of the conceptacle surface and indicate relationships between apparently differing structures.

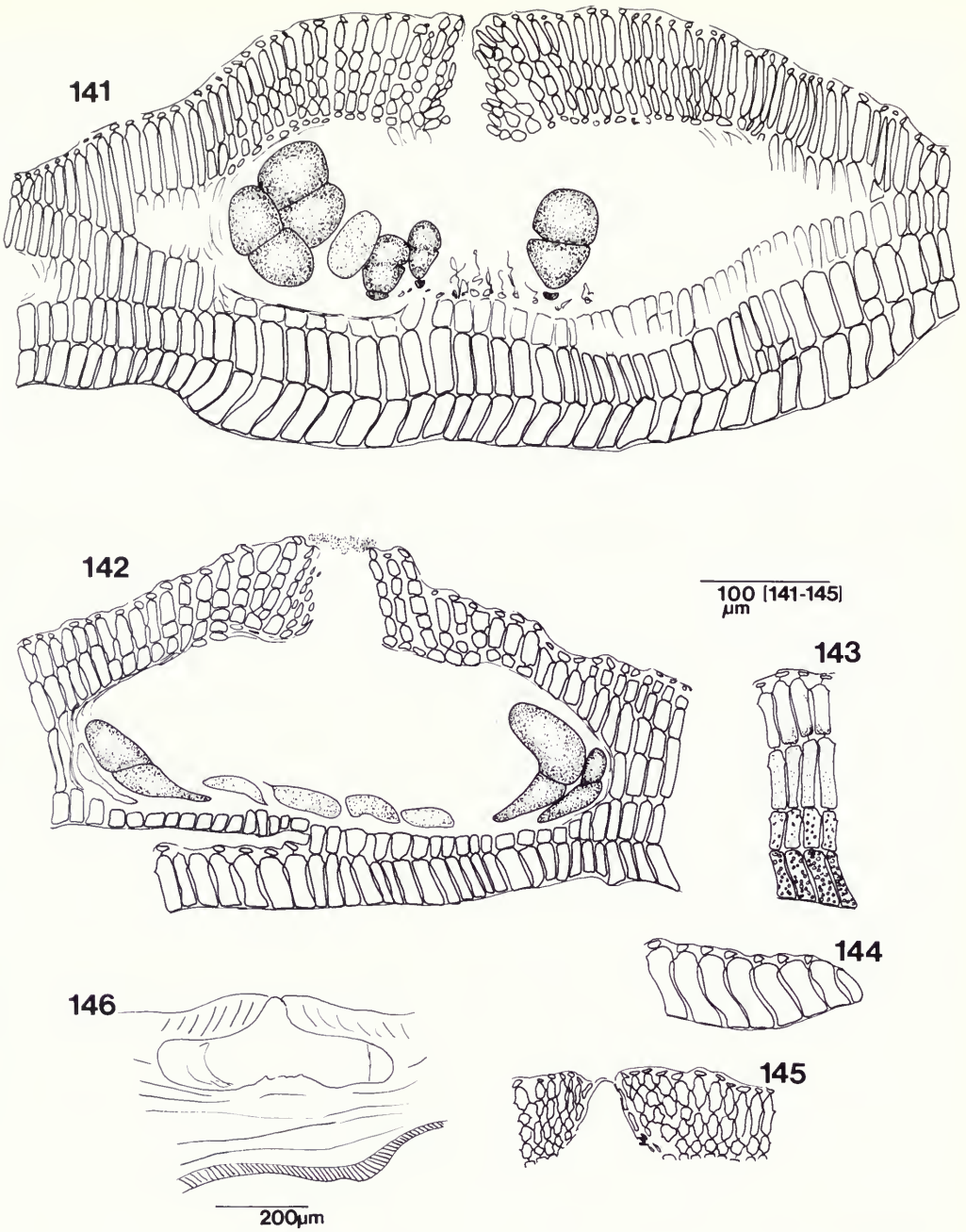
VEGETATIVE ANATOMY. In VS the thallus may show strongly aligned horizontal cell rows (Figs 52c, 104, 126), as seen in the type specimen of *Melobesia hapalidioides* (Figs 8, 101, 105), or more sinuate rows (Figs 103, 129, 146). Axial cells vary from being quite short and more or less vertically orientated (Fig. 52c) to tall and obliquely orientated (Figs 103, 104, 128, 141); they are often full of starch grains (Fig. 104) which may measure up to 6 μm diameter. Short, straight palisade cells are regarded as characteristic of var. *macrocarpum* (e.g. Hamel & Lemoine, 1953—as *hapalidioides*), but tall oblique ones also occur commonly and on average the height is about two and a half times the diameter.

Erect filaments are up to 14 cells long (Figs 52c, 103, 126)



Figs 135–140 To show features of British Isles plants of *Titanoderma pustulatum* var. *macrocarpum* (scales in μm unless stated).

135. Conceptacles of plant from Kimmeridge (86/159c) growing on *Laminaria* holdfast with shed spores (arrow) on the surface (see also Fig. 15).
136. Ostiole and bulbously calcified roof cells with trichocytes (arrow) from Fig. 135.
137. Epilithic plant of var. *macrocarpum* (M) from Lulworth (86/135) overgrowing the imbricating growth form (B), *Lithophyllum incrustans* (L) overgrows both plants.
138. Conceptacle of epilithic plant from Kimmeridge (87/12) with a central dome and released bisporangia on the surface.
139. Surface of the central part of the thallus (87/12) showing calcareous ridges encircling epithallial cells (e) in various stages of shedding.
140. Surface of thallus margin (87/12) showing elongated axial cells (a) and epithallial concavities (e).



Figs 141–146 Vertical sections of *Titanoderma pustulatum* var.*macrocarpum*.

141. Bisporangial conceptacle (83/380).

142–143. Bisporangial conceptacle and thallus cells of lectotype of *Melobesia simulans* (see Fig. 108). Starch grains in Fig. 147 gradually mature towards the thallus base.

144. Bistratose thallus margin (83/233).

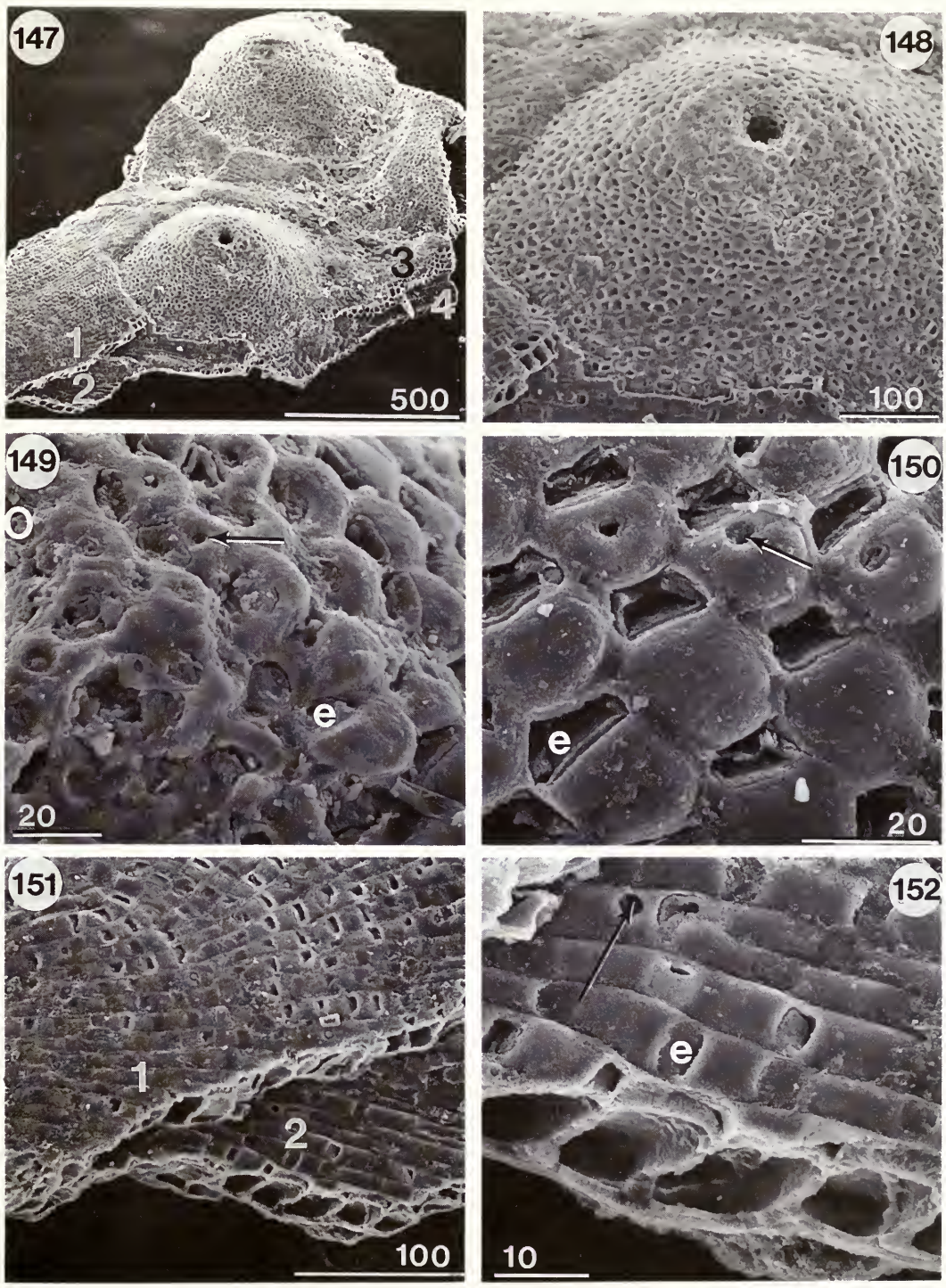
145. Ostiole and adjacent roof filaments of *L. adplicitum* in Fig. 146.

146. Diagrammatic drawing to show characteristic shape of bisporangial conceptacle of *Lithothamnion adplicitum* (BM), now included in var. *macrocarpum*.

and lower cells are usually full of starch grains; secondary pit connections are often conspicuously tube-like. Epithallial cells are triangular at the thallus margin (Fig. 144) and flattened in older parts of the thallus. Epithallial shedding, as seen in the lectotype (Fig. 107), probably occurs frequently (see p. 16).

Plants often regenerate extensively (Figs 103, 129) causing patches of axial filaments to mingle with erect filaments as the thallus overgrows senescent areas of itself, or weaves among worm tubes and other irregularities of the substratum.

BISPORANGIAL PLANTS. Conceptacles vary from low conical to domed (Figs 55, 135–138) and conceptacle chambers (Figs 52b-d, 125, 129, 141) are usually shallowly elliptical. The

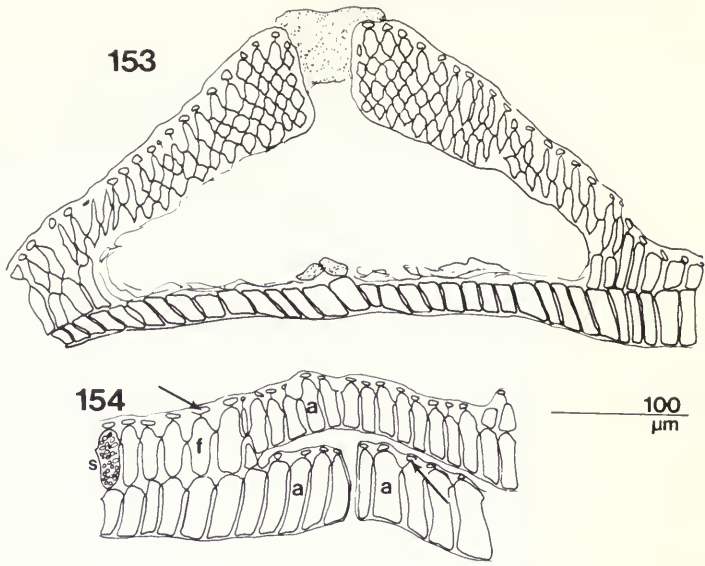


Figs 147–152 Imbricating growth form of *Titanoderma pustulatum* var. *macrocarpum* from Lulworth, Dorset (86/135) (scales in μm).

147. Showing two bisporangial conceptacles and various thallus lobes (1–4).
148. Bisporangial conceptacle.
149. Conceptacle roof (from Fig. 148) immediately below ostiole (o) with epithallial concavity (e) and trichacyte (arrow).
150. Further down conceptacle showing heavily calcified, stepped cells with epithallial concavities (e) and trichocytes (arrow).
151. Two superimposing thallus lobes (1 & 2).
152. Detail of thallus surface and VS showing axial cells (a), epithallial concavities (e) and trichocyte (arrow).

conceptacle roof is generally three cells thick peripherally (Figs 52b-e, 131, 141), it thickens towards the ostiole where the roof filaments may be up to seven cells long (Figs 52b-e, 130, 133, 145) and small papillae may line the ostiole canal (Fig. 141). The structure of the conceptacle roof, particularly near the ostiole, agrees with that seen in type material of *Melobesia hapalidioides* (Figs 100, 105), *M. simulans* (Fig. 117), and *M. macrocarpa* (Fig. 52b), and also with conceptacles illustrated by Suneson (1943, figs 22, 23, pl. VII, fig. 37—as *Lithophyllum pustulatum*). Bisporangia (Figs 52c-e, 141) are borne peripherally and are often very abundant, perhaps up to 80 per conceptacle. They are generally twice as long as wide, and are rather small compared with var. *pustulatum* (Table 1). There is usually a small columella (Figs 52c, 141), although Rosanoff (1866, pl. IV, fig. 15 ; see Chamberlain, 1986, fig. 22) illustrated a dense mass of swollen, paraphysis-like cells forming the columella and growing from the roof in the type material of *Melobesia macrocarpa*. A conceptacle from this material is illustrated (Fig. 52b) but the paraphyses have shrivelled in the dried material.

Old conceptacles may either become filled in, or, as in the type specimen of *Lithothamnion adplicitum* (Fig. 146), become immersed in the thallus (Fig. 132). Plants strongly resembling *'L. adplicitum'* have been observed in other subtidal locations in central southern England, notably Adey's from the Isle of Wight (70–6–B, 70–6–E, USNC!) (Figs 131, 132).



Figs 153–154 Vertical sections of the imbricating growth form of *Titanoderma pustulatum* var. *macrocarpum*.
153. Bisporangial conceptacle (83/162).
154. Imbricating thalli (78/199) showing limited development of erect filaments (f) from which axial filaments (a) regenerate. All cells except the epithallial cells (arrows) are full of starch grains (s).

VARIATION RANGE. Plants now attributed to var. *macrocarpum* show a considerable range of variability, including an imbricating growth form which will be described in detail, and three less defined groups of plants:

(1). Flat, rose-pink, non-imbricating, epiphytic plants occurring almost exclusively on *Phyllophora*. These plants conform to the type specimen of *Melobesia macrocarpa* (Fig. 52b). Examples: 76/83, 76/84.

(2). Reddish or orangish plants forming flat or partly imbricating thalli growing on stones, shells, maerl, etc. (Figs 52c, 54). These plants have strongly horizontally aligned thallus cell 'rows' and often show areas of short, vertically orientated axial cells. Calcification of the side walls of the thallus cells is particularly thick, causing secondary pit connections to appear tube-like; large starch grains (to 6 µm diameter) are very common in lower thallus cells. The cells of the roof filaments of bisporangial conceptacles are usually vertically orientated. These plants conform to type material of *M. hapalidioides* (Fig. 105). Examples: 84/229, 87/58.

(3). Mauvish plants forming flat or partly imbricating thalli growing on stones, shells, etc. (Figs 52d, 129, 130, 133, 141). These plants usually have somewhat sinuate thallus cell 'rows' and entirely obliquely orientated axial cells. Calcification of side walls is not particularly thick and starch grains are not noticeably large. The roof filaments of bisporangial conceptacles often slope markedly towards the ostiole canal. These plants conform to type material of *M. simulans* (Fig. 142). Examples: 83/233, 84/229, 84/311, 86/135, 86/159, 87/12, 87/13.

(4). Imbricating growth form: rose- to salmon-pink plants growing on stones and shells, composed of up to five, mainly bistratose imbricating thallus layers (Figs 151, 152), collective thalli are up to *c*20 mm diameter but it is impossible to determine the extent of any individual plant. The thallus grows over and around the conceptacles (Fig. 147) and forms fan-like lobes. In surface view (Fig. 152) thallus lobes are composed of radiating axial filaments with long cells and short epithallial concavities; occasional trichocytes occur.

In VS the thallus mainly comprises bistratose layers of more or less oblique axial cells and triangular epithallial cells (Figs 52e, 154). Locally the thallus thickens to produce one- or two-celled erect filaments (Figs 52e, 154) from which new imbricating lobes develop. Thallus cells are often packed with large starch grains up to 6 µm diameter.

Bisporangial conceptacles (Figs 147, 148) emerge abruptly and are strongly conical, they have a stepped surface (Figs 149, 150) and trichocytes occur commonly. In VS (Figs 52e, 134, 153) the conceptacle chamber is broadly triangular and the roof thickens very conspicuously round the ostiole where it comprises vertically orientated filaments up to seven cells long. The roof cells have characteristically diamond-shaped lumens and tube-like secondary pit connections. Bisporangia are borne peripherally, with up to *c*. 60 per conceptacle.

Imbricating plants usually occur in company with other forms of var. *macrocarpum* (Fig. 137) and are overgrown by them. A characteristic example of this growth form occurs with the type of *Lithothamnion adplicitum* (Fig. 120). Examples: 83/233, 86/135.

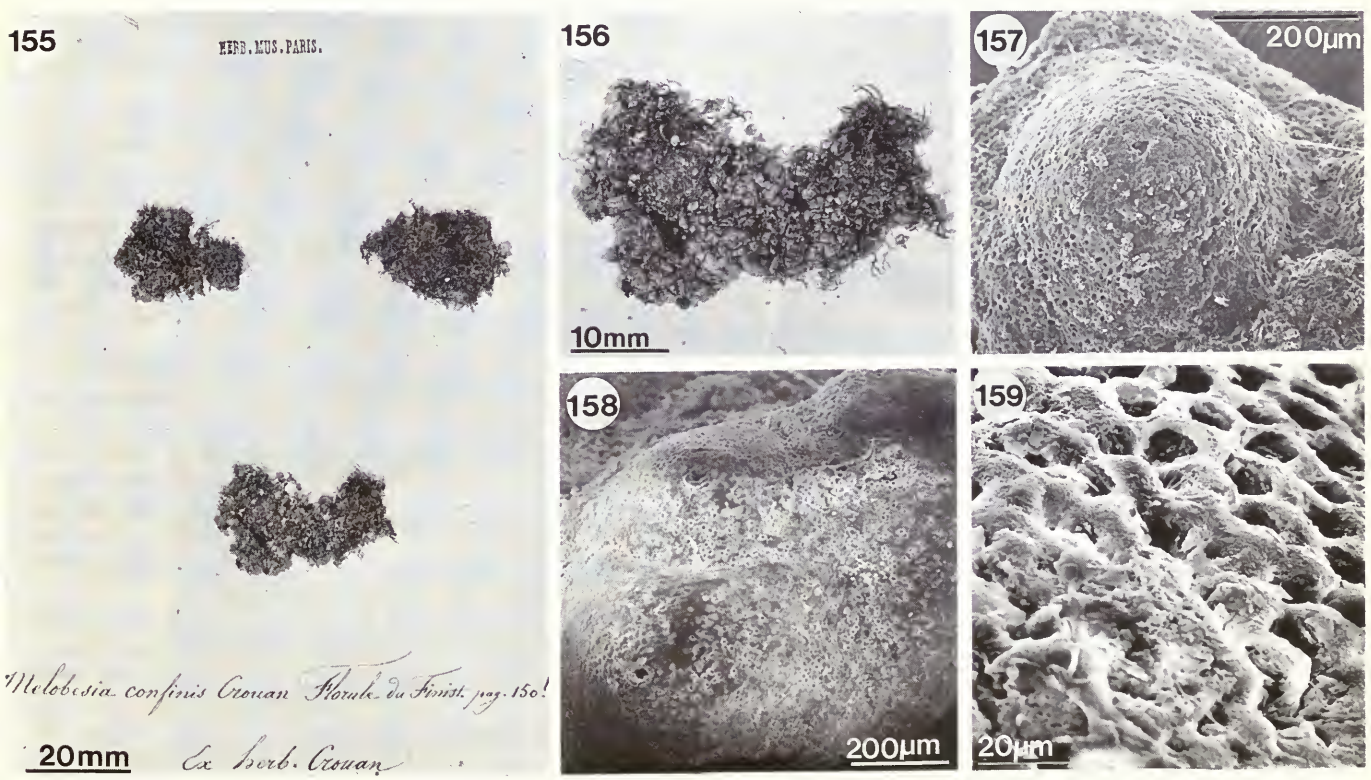
DISTRIBUTION. *British Isles*: Confirmed from Northumberland, Sussex, Hampshire, Dorset, Devon, Cornwall, Jersey, Dyfed, Isle of Man, Co. Clare, Co. Mayo. *World*: Norway (fide Rueness, 1977, as *Dermatolithon hapalidioides*), Sweden, western France, Mediterranean, Canary Islands, southern Australia.

HABITAT AND PHENOLOGY. Growing mainly on rocks, pebbles, maerl, shells and other marine animals, occasionally epiphytic—usually on *Phyllophora*. This variety occurs mainly subtidally (Adey & Adey, 1973: 249—as *Tenarea*) and is recorded down to 70–90 m depth (USNC! Adey 70–11–A), but also occurs in low intertidal rock pools. It has been found

quite commonly in southern England and Wales, usually in small amounts. Bisporangia have been observed throughout the year.

HERBARIUM SPECIMENS CONFIRMED AS T. PUSTULATUM VAR. MACROCARPUM. As *Lithophyllum (Dermatolithon) hapalidioides*, British Isles, Co. Mayo, Clew Bay, dredged, on shells and pebbles, 20 February 1911, *A. D. Cotton*, det.Mme P.Lemoine (1913*b*) (BM Box 915!) (Fig. 86); British Isles, Co. Mayo, Clew Bay, dredged, on *Patella*, March 1911, *A. D. Cotton*, det. Mme P.Lemoine (1913*b*) (BM Box 920!) (Fig. 85); Turkey, Ile Tenedos, 5 August 1910, det. Mme P. Lemoine (1915) (PC!); France, Rance, St-Servan, Pointe de Cancaval, 8 m de profondeur, 1930, *M. Lami*, det.Mme P.Lemoine (PC); as *Dermatolithon adplicitum*, British Isles, Devon, Plymouth, dredged, March 1909, *E. M. Holmes, Alg.Brit.rar.Exsicc.* XII, no. 284, (BM!); as *Lithothamnion strømfeltii* f. *tenuissima*, British Isles, Devon, Plymouth, on shells, March 1896, *E. A. Batters*, (BM Box 573!); as *Melobesia simulans*, France, M la Ninon, 24 February 1859 and Rade de Brest, dredged, 3 January 1862, *P.-L. & H.-M. Crouan* (CO!) (Fig. 109); as *Melobesia pustulata*, Italy, Livorno, on '*Acanthatylo heredia*' [*Phyllophora*], *Meneghini*, herb. Kützing (L 940.317.500!); as *Tenarea hapalidioides*, British Isles, SW Wales, between Skomer and the mainland, 70–90 m depth, 18 December 1970, *W. H. Adey*, 70–11–A, (USNC!); British Isles, Hampshire, off Isle of Wight, 0–30 m depth, 30 November 1970, *W. H. Adey*, 70–6–B and 70–6–E, (USNC!) (Figs 131, 132); as *Lithophyllum pustulatum*, Sweden, Kristineberg, Bohuslan, on *Phyllophora rubens*, 30 June 1949, *S. Suneson* (LD! and his personal collection!) (Figs 118, 119); British Isles, Devon, Pridmouth, on *Phyllophora*, 24 May 1886, *R. V. Tellam*, (BM!); British Isles specimens in herb. *Chamberlain*: Dorset, Chapman's Pool, 7 m depth, on *Phyllophora pseudoceranoides* and *P. crispa*, 30 May 1976, 76/83–84; Dorset, The Fleet, on stones, 1–2 m depth, 22 January 1983, 83/72; Dorset, Lulworth, on a stone, 3–5 m depth, 15 March 1983, 83/233; Isle of Man, Cronk ny Iree Laa, on maerl, 18 m depth, 20 March 1984, 84/158; Hampshire, Princess's Shoal, off Bembridge, on stones, 11 m depth, 15 May 1984, 84/229; Dorset, Kimmeridge, on a stone, low tide, 28 August 1984, 84/311; Dorset, Lulworth, on a stone, 1–2 m depth, 9 September 1986, 86/135; Dorset, Lulworth, on *Laminaria hyperborea*, 2–3 m depth, 8 November 1986, 86/159; Dorset, Kimmeridge, on stones, intertidal, 1 February 1987, 87/12–13; Hampshire, Isle of Wight, on a stone, 8–10 m depth, 11 July 1987, 87/58. *Imbricating growth form*: Jersey, St Catherine's Pier, on a stone, 10 m depth, April 1982, 83/162; Cornwall, St Mawes, on a shell, subtidal, 2 July 1985, 85/102; Dorset, Lulworth, on a stone, 1–2 m depth, 9 September 1986, 86/135.

HERBARIUM SPECIMENS MISIDENTIFIED AS T. PUSTULATUM VAR. MACROCARPUM. As *Dermatolithon hapalidioides*, Faeroes, Kvanhauge, on *Patella*, 7 May 1896, *F.Børgesen* (C!) (Fig. 60) (= var. *pustulatum*); British Isles, Berwick, on *Corallina* and *Gelidium* turf, 29 January 1887, *E. A. Batters* (BM!) (= var. *confine*).



Figs 155–159 Lectotype specimen of *Melobesia confinis* (PC) and *Le Jolis* 275 (BM).
155. Lectotype specimen (central strip of mounting paper omitted).
156. Enlargement of lower sample from Fig. 155.
157. Bisporangial (presumed) conceptacle from Fig. 156.
158. Spermatangial conceptacles from Fig. 156.
159. Bisporangial conceptacle roof showing ridged structure seen from above, *Le Jolis* 275.

1c. **Titanoderma pustulatum** var. **confine** (P. & H. Crouan) Y. Chamberlain, **comb.nov.**—*Melobesia confinis* P. & H. Crouan, *Fl. Finistère:* 150 (1867).—*Dermatolithon hapalidioides* f. *confinis* (P. & H. Crouan) Foslie in *K.nor. Vidensk.Selsk.Skr.* **1899**(7): 12 (1900).—*Lithophyllum hapalidioides* f. *confinis* (P. & H. Crouan) Foslie in *K.nor. Vidensk.Selsk.Skr.* **1905**(3): 128 (1905).—*Tenarea confinis* (P. & H. Crouan) W. & P. Adey in *Br.phycol.J.* **8**: 393 (1973).—*Dermatolithon confinis* W. & P. Adey in Parke & Dixon, *J.mar.biol.Ass.U.K.* **56**: 534 (1976), invalid. (Art. 33.2).—*Titanoderma confine* ['*confinis*'] (P. & H. Crouan) J. Price, D. John & G. W. Lawson in *Bull.Br.Mus.nat.Hist.* (Bot.) **15**: 86 (1986). Type: No locality data but presumably from Finistère, ex herb. Crouan (PC!—lectotype selected here) (Figs 155–158).

Figs 52f,g,h, 155–204.

Lithophyllum pustulatum f. *intermedia* Foslie in *K.nor. Vidensk. Selsk. Skr.* **1905**(3): 117 (1905).—*Lithophyllum macrocarpum* f. *intermedia* (Foslie) Foslie in *K.nor. Vidensk.Selsk.Skr.* **1905**(3): 128 (1905).—*Lithophyllum litorale* Suneson in *Acta Univ.lund.* II, **39**: 36 (1943).—*Fosliella intermedia* (Foslie) G. M. Smith, *Mar. Alg. Monterey*: 226 (1944).—*Dermatolithon litorale* (Suneson) Hamel & Lemoine in *Archs Mus.natn.Hist.nat.Paris* VII, **1**: 66 (1953).—*Titanoderma litorale* (P. & H. Crouan) Cormaci & Furnari in *Taxon* **36**: 757 (1987). Type: As *Lithophyllum pustulatum* f. *intermedia*, Denmark, Hirtsholm, on *Fucus*, 21 September 1893, *L. K. Rosenvinge* 4116. (C!—lectotype selected here by A. Athanasiadis & Y. Chamberlain). (Figs 164, 165).

Lithophyllum pustulatum f. *ascripticia* Foslie in *K.nor. Vidensk. Selsk. Skr.* **1906**(8): 33 (1907).—*Dermatolithon ascripticium* (Foslie) Setchell & Mason in *Proc.natn. Acad.Sci.* U.S.A. **29**: 96 (1943).—*Fosliella ascripticia* (Foslie) G. M. Smith, *Mar. alg. Monterey*: 224 (1944).—*Dermatolithon pustulatum* f. *ascripticium* (Foslie) Dawson in *Pacif.Nat.* **2**: 32 (1960).—*Tenarea ascripticia* (Foslie) Adey in *K.nor. Vidensk.Selsk.Skr.* **1970**(1): 6 (1970). Type: U.S.A., California, Monterey, on *Nitophyllum ruprechtianum*, 10 January 1899, *Gibbs* (TRH—lectotype).

ILLUSTRATIONS. As *Lithophyllum macrocarpum* f. *intermedia*, Nichols in *Univ.Calif.Publs Bot.* **3**: pl. II, fig. 12, pl. 12, figs 15–17 (1909); Rosenvinge in *K.dansk. Vidensk.Selsk.Skr.* VII, **2**: figs 184, 185 (1917); as *Lithophyllum pustulatum* f. *ascripticia*, Nichols in *Univ.Calif.Publs Bot.* **3**: pl. 10, figs 2, 3, pl. 11, fig. 10; pl. 12, figs 18–20 (1909); as *Lithophyllum hapalidioides* f. *confinis*, Lemoine in *Archs Mus.natn.Hist. nat.Paris* V, **5**: 137, fig.3 (1913); Foslie [ed.Printz], *Contrib. Lithothamnia*: pl. LXXII, fig.7 (1929); as *Lithophyllum litorale*, Suneson in *Acta Univ.lund.* II, **39**: figs 20, 21, pl. VIII, fig. 39 (1943); as *Dermatolithon litorale*, Chamberlain in *Phycologia* **17**: figs 1, 2, 4, 5, 8 only (1978).

DESCRIPTION. Plants epiphytic or growing on rocks, pebbles, and shells, from flat, adherent to loosely attached, frequently extensively imbricating, to 30 mm diameter, to 620 (900) μm thick, tapering to an often extensive bistratose margin, adjoining plants often overgrowing one another, mauvish to blueish/violet, often becoming bleached, chalky, surface smooth or patchy due to areas of regeneration. Single layer of *axial filaments* with cells obliquely orientated and usually sinuate, cells 25–179 μm high × 11–22 μm long, *erect filaments* absent to 14 cells long, cells 14–93 μm long × 9–24 μm diameter, *epithallial cells* triangular, rectangular or domed, cell contents usually sparse, starch grains uncommon, new axial filaments often regenerating from cells of erect filaments to form thallus lobes, trichocytes occurring occasionally in axial and erect filament cells. *Gametangial and tetraspsorangial plants* not seen; *bisporangial conceptacles* widely spaced to densely crowded, rounded-conical, mainly arising abruptly from thallus surface with well-defined conceptacle periphery, 400–500 μm external diameter, conceptacle surface ridged to stepped, conceptacle chamber hemispherical to elliptical, 234–416 μm diameter, 91–234 μm high, roof 29–62 μm thick, roof thickening to 3–5 cell layers near ostiole with cells irregularly sized, columella slightly- to well-developed, up to *c.* 60 bisporangia (occasional stunted tetrasporangia seen), 62–104 μm long × 26–52 μm diameter, old conceptacles either becoming infilled or buried in the thallus. [Minute growth form described under variation range, see p. 57]

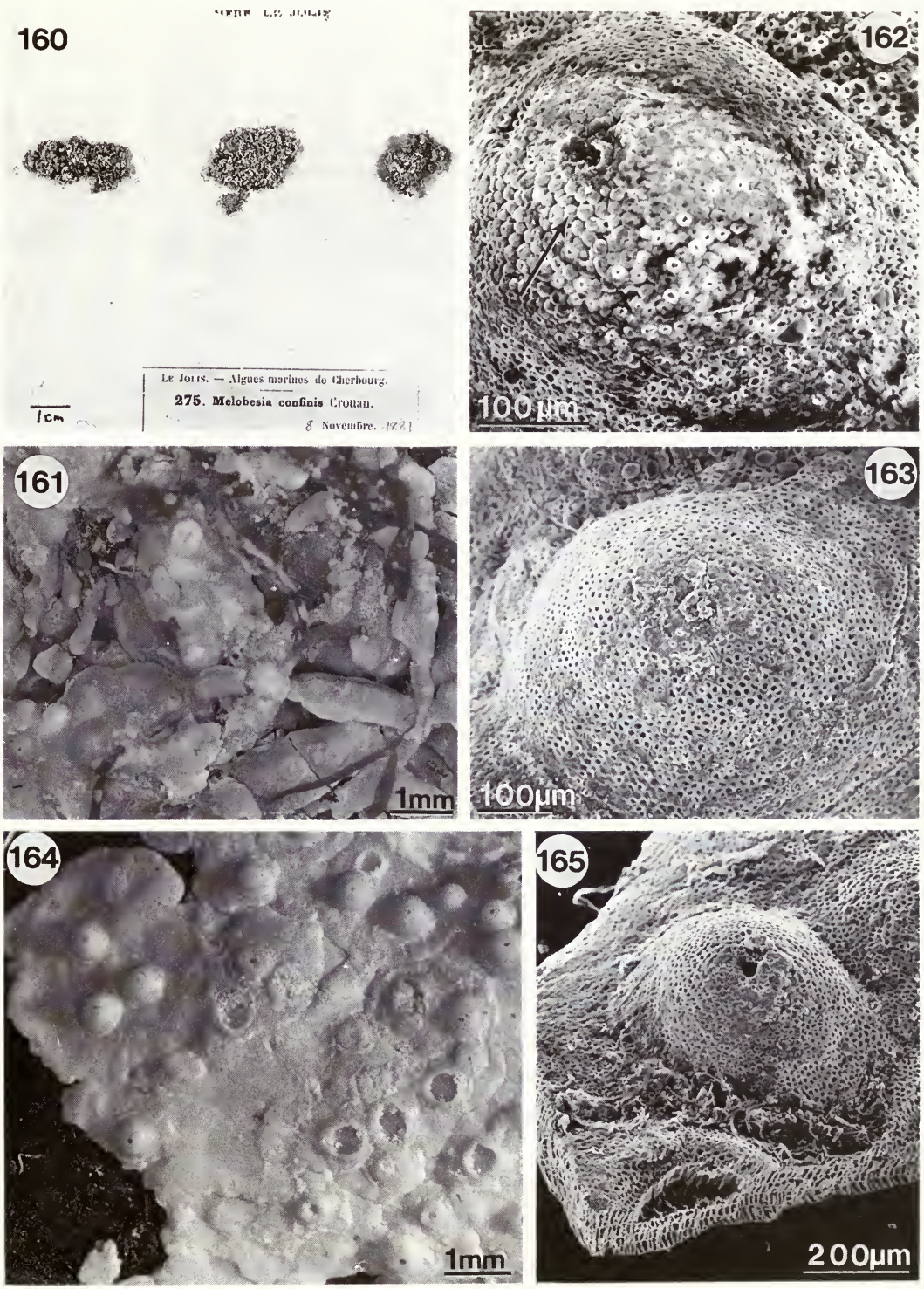
HISTORICAL. The Crouan brothers (1867) described *T. pustulatum* var. *confine* (as *Melobesia confinis*) as being pale violet, 1–2 cm diameter, thin, hard, lobed; with cells two to three times as long as wide in surface view and four to six times in VS, the small hemispherical conceptacles contained bisporangia and keramidia (cystocarps) that were angular and fused together. It grew on corallines, *Patella*, etc. at low water. No specimen was found of this species at Concarneau and, therefore, on the advice of Dr Françoise Ardré, a mounted sheet of the Crouans' specimens (Fig. 155) in PC has been selected as lectotype. These specimens agree with the Crouans' description with the exception that the diameter they cite of 1–2 cm does not seem applicable to the small fragmentary crusts (Figs 155, 156) but possibly applies to each of the three mounted samples.

Foslie (1900*a*) examined some of the Crouans' specimens in PC in which *Melobesia confinis* grew on both balanoid shells and plants of *Gelidium corneum* attached to them. He said that this and similar material collected by Le Jolis (presumably no. 275) differed from *M. hapalidioides* principally by being a purplish grey colour. He therefore reclassified the taxon as *Dermatolithon hapalidioides* f. *confinis*, and subsequently transferred it to *Lithophyllum* (Foslie, 1905*a*: 128).

Lemoine (1913*b*) retained the name *L. hapalidioides* f. *confinis* when describing a plant growing on *Patella* at Clew Bay, Ireland (BM!) (Fig. 174), pointing out that two of the characteristics of f. *confinis* were the violet colour and frequently imbricating lobes. Later, Lemoine (1931) identified imbricating plants from St.-Servan as f. *confinis* and this record is repeated in Hamel & Lemoine (1953), but these plants, are now considered to be the imbricating growth form of *T. pustulatum* var. *macrocarpum*.

Adey & Adey (1973) recognized violet, crustose '*Dermatolithon*' plants with exceptionally tall, thin cells as a distinct species which they recombined as *Tenarea confinis* (P. & H. Crouan) W. & P. Adey. Unfortunately this was transmuted to the invalid combination *Dermatolithon confinis* W. Adey & P. Adey in Parke & Dixon (1976) and this name has subsequently been used by a number of British authors (e.g. Price, Hepton & Honey, 1981; Hardy, 1985). While the Adeys' (1973) dimension data agree with this study, I was not able to find any plants of var. *confine* in Adey's collection (USNC). One collection from rocks at low tide, at Wembury, Devon (no. 7–14, 1970) proved to be var. *pustulatum*.

A further taxon that I consider to be synonymous with var.



Figs 160–165 Herbarium specimens now attributable to *Titanoderma pustulatum* var. *confine*.

160. Specimen of *Melobesia confinis* distributed as *Le Jolis*, Alg. mar. Cherbourg 275 (BM).
161. Details of fragmentary thalli from Fig. 160.
162. Immature conceptacle from Fig.160 with bulbous epithallial cells (arrow).
163. Mature conceptacle from Fig. 160, bulbous epithallial cells have disintegrated leaving a slightly ridged roof surface.
164. Lectotype of *Lithophyllum pustulatum* f. *intermedia* Foslie (C).
165. Conceptacle from Fig. 164 (see Fig. 201).

confine was first described by Foslie (1905*a*: 117, 121) as *Lithophyllum pustulatum* f. *intermedia* (see p. 53 for lectotypification), before being reclassified as a form of *L. macrocarpum* later in the same paper (Foslie, 1905*a*: 128). This form was based on subtidal plants growing on *Fucus vesiculosus* L. and other hosts collected by Rosenvinge at various localities around Denmark. It was later described and illustrated by Rosenvinge (1917) himself, who recorded occasional cystocarpic plants among predominantly bisporangial populations.

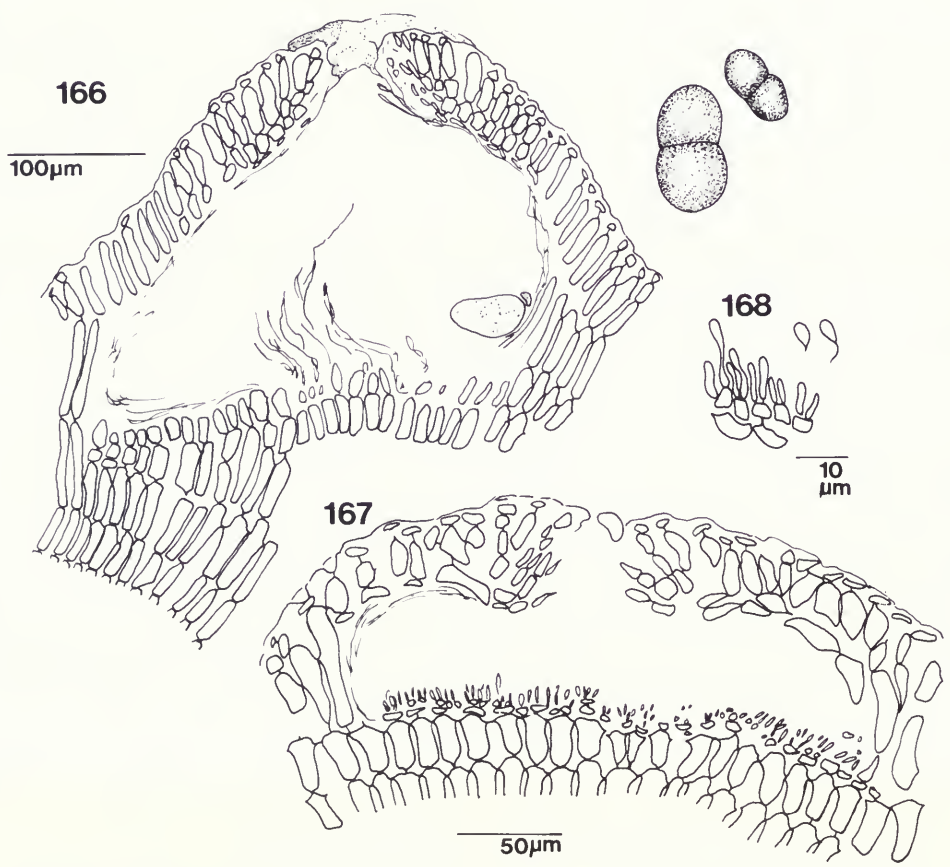
Suneson (1943) gave a detailed, illustrated description of further Scandinavian material of this taxon, from the Swedish west coast, under the new name of *Lithophyllum litorale*. He changed the name because he wanted to raise f. *intermedia* to species status, but another, quite different, species had already been named *L. intermedium* Foslie.

The known distribution range of *L. macrocarpum* f. *intermedia* was greatly extended when Foslie identified as this forma epiphytic specimens sent to him by Nichols (1909: 353) from La Jolla, California. Nichols (1909) described and figured this bisporangial material (UC!) which agrees closely with Rosenvinge's and Suneson's plants. Meanwhile Foslie (1907*b*) had described another epiphytic entity from California as *L. pustulatum* f. *ascripticia*; this plant had a thallus that was very similar to f. *intermedia*, having very tall, thin cells, but in this case tetrasporangial and gametangial conceptacles. Nichols (1909) also gave an illustrated description of f. *ascripticia* based on his own Californian material identified for him by Foslie, and I see no reason to doubt, on the basis of Nichols's material (UC!) and descriptions, that these formae both belong to the same taxon which is now subsumed in *T. pustulatum* var. *confine*.

Mason (1953) gave a description of *Dermatolithon ascripticium* (Foslie) Setchell & Mason (1943) based on Gibbs's type specimen from Monterey and a wide range of further material from California and Oregon and she suggested that f. *intermedia* was probably conspecific.

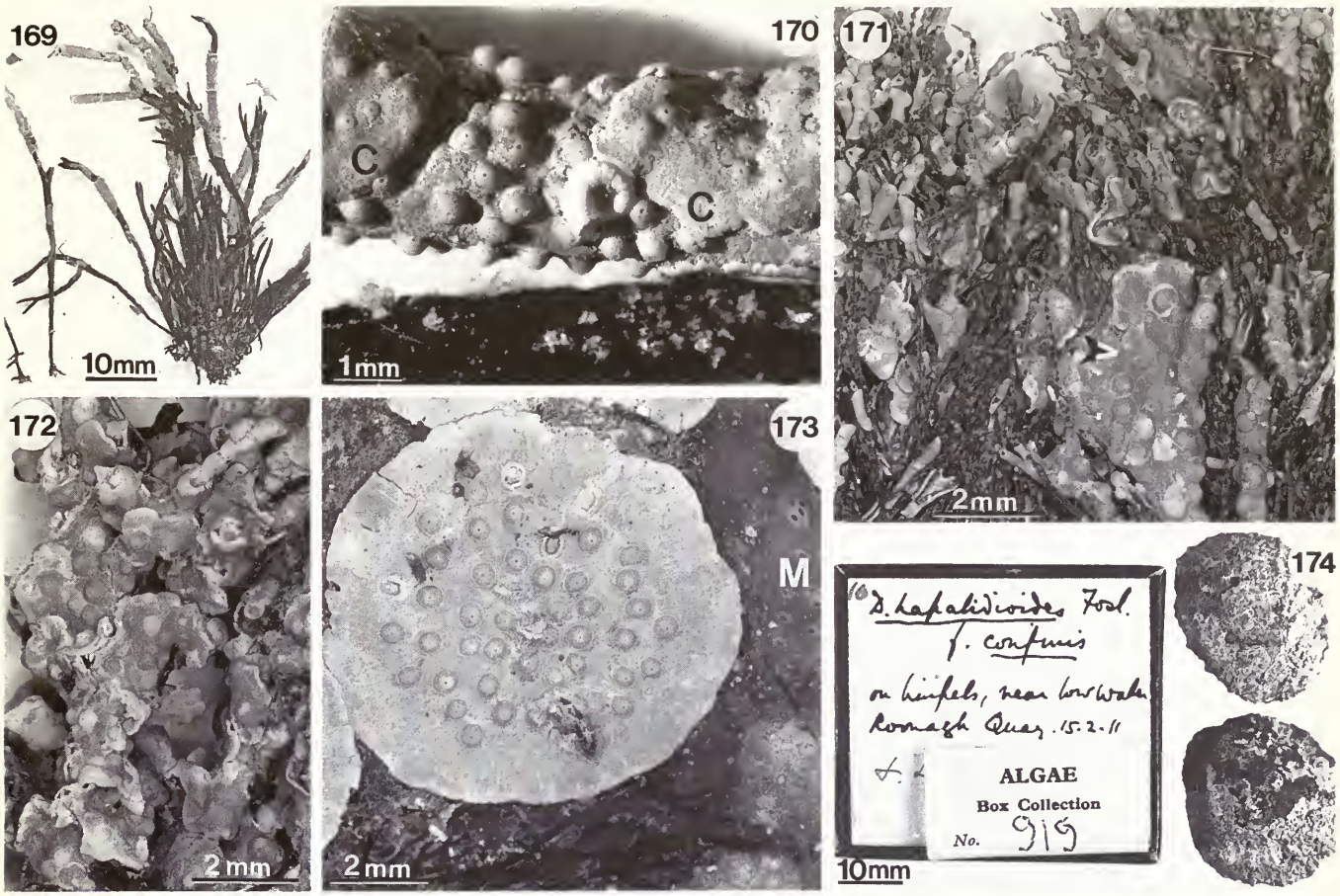
Ganesan's (1962) description of *Dermatolithon ascripticium* from south India agrees well with Nichols's description (1909).

The name *Dermatolithon litorale* (Suneson) Hamel & Lemoine has come to be applied to small *Titanoderma* plants with prominent conceptacles from the Mediterranean (e.g. van der Ben, 1969; Cormaci & Furnari, 1979); such records need confirmation because it is possible that they pertain to var. *canellatum* (see Chamberlain, 1986) rather than var. *confine*. The description of *D. litorale* in Hamel & Lemoine (1953) is based on Suneson (1943) and, therefore, refers to var. *confine*, but again their subsequent Mediterranean records require confirmation.



Figs 166–168 Vertical sections of *Titanoderma pustulatum* var. *confine*.

166. Bisporangial conceptacle and two extruded bisporangia from Le Jolis's exsiccata Alg. Mar. Cherbourg no. 275 (see Fig. 160).
167. Spermatangial conceptacle from lecototype of *Melobesia confinis* (PC) (see Fig. 158).
168. Details from Fig. 167 of elongate attached spermatangia and two released ones that are rounding off.



Figs 169–174 To show habit range of *Titanoderma pustulatum* var. *confine* in the British Isles.

169. On *Furcellaria lumbricalis* (80/105) from Bembridge.
170. Growing under *Titanoderma corallinae* (c) on *Furcellaria lumbricalis* (79/208) from Bembridge.
171. *Cladophora rupestris* (80/107) from Bembridge with *T. pustulatum* var. *confine* (arrowhead) and var. *canellatum* (arrow).
172. On the base of *Corallina officinalis* (84/399) from Port Cornaa, Isle of Man.
174. A thin plant on *Palmaria palmata* (86/153A) from Wembury, *Melobesia membranacea* (M) is also present.
174. Clare Island Survey specimen (BM) growing on limpets. The handwriting is A. D.Cotton's, the plant was identified by Mme P. Lemoine.

NOTES ON TYPE AND OTHER HISTORICAL SPECIMENS. (1). *Melobesia confinis* P. & H. Crouan (1867: 150). Lectotype (now designated): no locality data but presumably from the region of Finistère, ex herb. Crouan (PC!). (Figs 14, 155–158, 167, 168, 197).

The lectotype (Figs 155, 156) comprises three samples of *Melobesia confinis* plants growing on an algal turf including *Corallina officinalis* and *Gelidium pusillum* interspersed with fragments of *Phymatolithon lenormandii* and small shells. The pale violet, crustose plants are very fragmentary and characteristically grow over and around the turf organisms. Few conceptacles are present, a presumed bisporangial conceptacle (Fig. 157) is abruptly emergent and conical, and measures *c.*400 µm external diameter. Spermatangial conceptacles (Fig. 158) measure *c.*400 µm externally, they are rounded and slightly protuberant, with a noticeable rim round the ostiole.

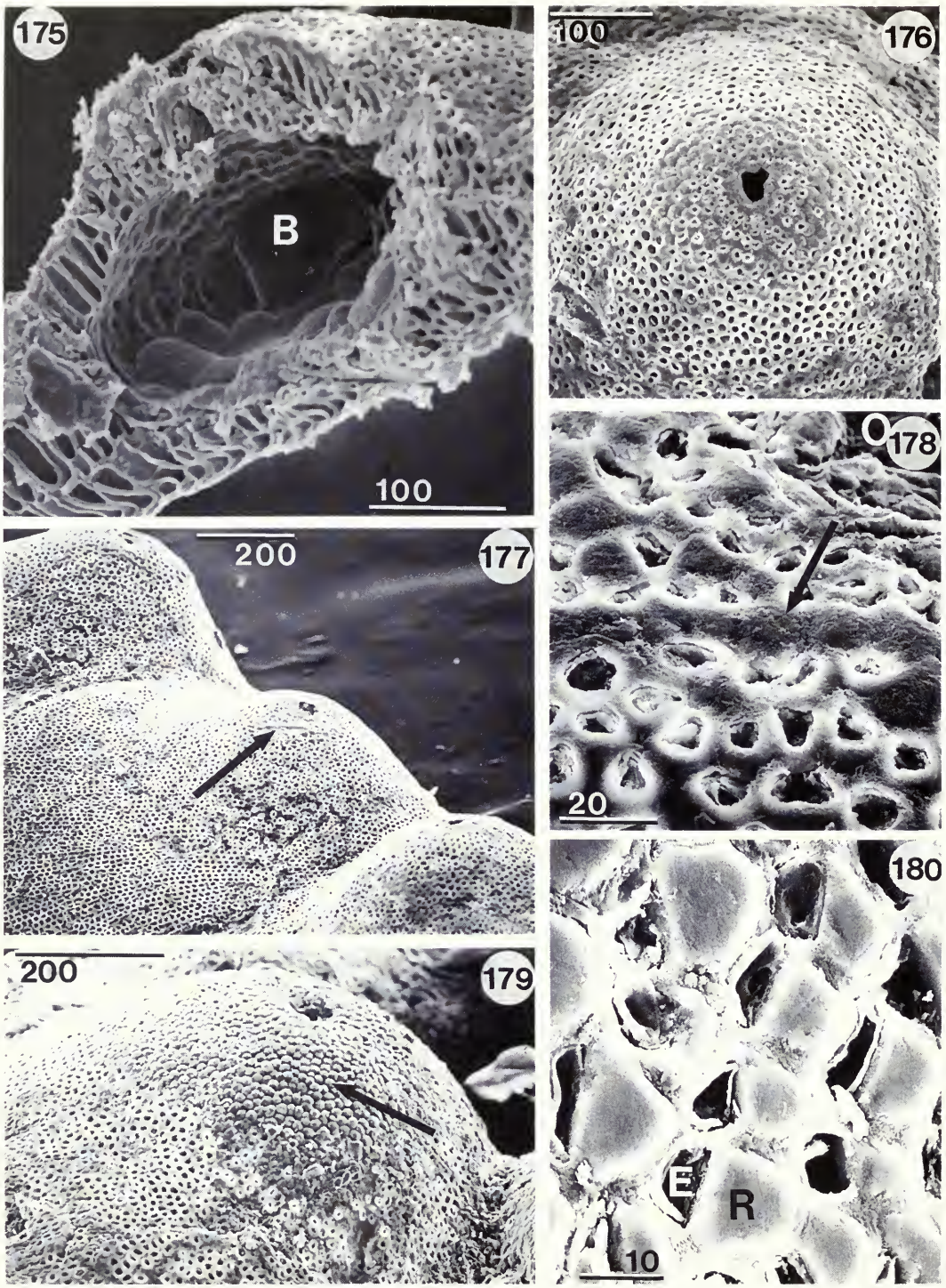
In VS (Fig.14) the thallus is up to 260 µm thick, and composed of tall, thin, oblique, axial cells measuring 28–88 µm high × 8–16 µm long and erect filaments up to six cells long with cells 13–54 µm long × 7–15 µm diameter. Frequent regeneration occurs (Fig. 14) as the thalli weave among the turf components. Spermatangial conceptacles (Figs 158, 167, 197) occur at the thallus surface with wide shallow chambers measuring *c.*240 µm diameter × 55 µm high. The conceptacle roof is mainly three cells thick including the epithallial cell, with the lowermost cell often horizontally elongated. The roof thickens to form filaments of small cells round the ostiole (Fig. 197). Spermatangia are borne across the floor of the conceptacle, when attached they measure about 7–15 µm long, rounding off when released (Fig. 168).

(2). *Melobesia confinis* P. & H. Crouan. France, Cherbourg, 8 November 1881, *Le Jolis, Alg.mar.Cherbourg* 275 (Figs 160–163, 166).

The appearance, habit, structure, and size of the plants in this widely distributed exsiccata (e.g. BM!, CHE!, PC!) are very similar to the lectotype of *Melobesia confinis*. All the specimens I have seen show the characteristics of var. *confine* and can be taken to exemplify that variety, thus constituting a widely available reference point.

(3). *Lithophyllum pustulatum* f. *intermedia* Foslie (1905*a*: 117). Lectotype (now designated by A. Athanasiadis and Y. Chamberlain): Denmark, Hirtsholm, on *Fucus*, 21 September 1893, *L. K. Rosenvinge* 4116 (C!) (Figs 164, 165, 201).

Foslie (1905*a*) based his description of f. *intermedia*



Figs 175–180 Scanning electron micrographs to show conceptacle variability in British Isles populations of *Titanoderma pustulatum* var. *confine* (scales in μm).

175. Vertical fracture of conceptacle containing bisporangia (B) from plant growing on *Laurencia pinnatifida* at Kimmeridge (80/66).

176. Conceptacle from same plant as Fig. 175. Note the similarity with the lectotype (Fig. 157) and *Le Jolis* 275 (Fig. 163).

177. Typically blunt, cone-shaped conceptacles from a plant growing on *Furcellaria lumbricalis* at Bembridge (79/208). Note characteristic strips of surface covering (arrow).

178. Detail of conceptacle in Fig. 177. A strip of surface covering (arrow) occurs below the ostiole.

179. Young conceptacle from epilithic plant, Isle of Man (84/147), bulbous epithallial cells (arrow) occur at conceptacle top.

180. Stepped conceptacle roof surface from plant growing at Rhoscolyn, Wales (78/329), with heavy calcified caps on the roof cells (R) cradling the epithallial concavities (E) (see Fig. 203).

principally on Danish plants collected by Rosenvinge. Material of this forma is very scanty in TRH. A lectotype was, therefore, chosen by Dr Athanasiadis and myself, from among Rosenvinge's specimens in C; no. 4116 bears an annotation by Foslie himself. The lectotype comprises fronds of *Fucus vesiculosus* covered with a mass of mainly thin thalli (Fig. 164) with abruptly emergent, conical, bisporangial conceptacles (Fig. 165). In VS (Fig. 201) the thallus is composed of oblique axial cells and erect filaments up to two cells long; the conceptacle roof is mainly three cells thick. The material resembles that from Sweden described by Suneson (1943—as *Lithophyllum litorale*) which is characterized by having particularly thin thalli.

PLANT APPEARANCE. *T. pustulatum* var. *confine* varies in appearance depending upon the substratum, although young plants form more or less orbicular, applanate thalli. Older plants may be many cells thick centrally, always with a more or less extended bistratose margin (Fig. 192). The lectotype material (Fig. 156) comprises small, fragmentary, lobed thalli growing amongst turf organisms. This style of growth is very common (Figs 171, 172), with the crusts often forming a complete sleeve round terete thalli of such algae as *Gelidium* and *Corallina*. Plants growing on *Furcellaria* (Figs 169, 170, 186) and other larger algae tend to have a smoother-looking surface, but with surface markings indicating the presence of underlying thallus regeneration. This feature is also evident in epiphytic Scandinavian material collected by Rosenvinge (C!, TRH!) and Suneson (his personal collection!) (Fig. 164), and Californian plants collected by Nichols (UC!). Adjacent plants may form a small crest where they meet (Fig. 164) but they do not overgrow each other. Plants growing on rocks, on old crustose coralline plants on rocks, or on shells (Fig. 174) are adherent and often form small nodules; they also show lobe-markings on the surface. Thin, smooth plants (Fig. 173) may occur on foliose algae. The blueish colour of var. *confine* in intertidal habitats may often be very striking enabling even minute plants growing amongst other crustose algae to be located.

In surface view the thallus shows elongate axial cells and epithallial concavities that are longer than wide (Fig. 183) at the margin, and honeycomb-like ridges with more or less circular epithallial concavities (Fig. 29) towards the centre; trichocytes (Fig. 29) occur infrequently. The thallus margin curls under at the extreme edge (Fig. 184).

All growth forms have more or less conical bisporangial conceptacles (Figs 170–173, 176, 177, 185–187) usually with rounded tops. The surface of the bisporangial conceptacle roof varies in different populations from stepped to rather smooth. The young conceptacle roof (Fig. 179) has bulbous epithallial cells but as it matures, calcification usually becomes lightly ridged (e.g. Figs 44, 159, 178), although not uniformly honeycomb-like as in var. *pustulatum*; often a smooth surface covering develops over the roof cells (Fig. 178). Occasionally a stepped surface develops (Fig. 180).

VEGETATIVE ANATOMY. *Titanoderma pustulatum* var. *confine* is characterized by having relatively tall, thin thallus cells (Figs 14, 52g, 181, 182, 199, 200), and axial cells are particularly tall (Fig. 199). There is nearly always a more or less extensive, bistratose margin (Fig. 192) and some plants may lack erect filaments throughout as was also found by Suneson (1943: 37). Erect filaments, up to 14 cells long, may be aligned, particularly in *Furcellaria* epiphytes. Frequently nodules composed of erect filaments develop (Fig. 181) or regeneration of axial filaments occurs (Figs 14, 199, 200) to form a complicated series of interweaving lobes (Fig. 196), especially in *Corallina* epiphytes and plants growing on shells, a feature also depicted by Cabioch (1972: 193, fig. A, as *Dermatolithon cystoseirae*).

Epithallial cells vary from triangular to domed and signs of shedding (Fig. 199) are seen. Thallus cells vary from being deeply pigmented to appearing almost empty when sectioned and stained; starch grains do not occur very often. Small trichocytes occur occasionally, particularly in summer. They develop as small cells attached to subepithallial initials (Fig. 15), as noted also by Rosenvinge (1917: 264) and Suneson (1943: 37); they are more frequent in var. *confine* than other *Titanoderma* taxa in the British Isles.

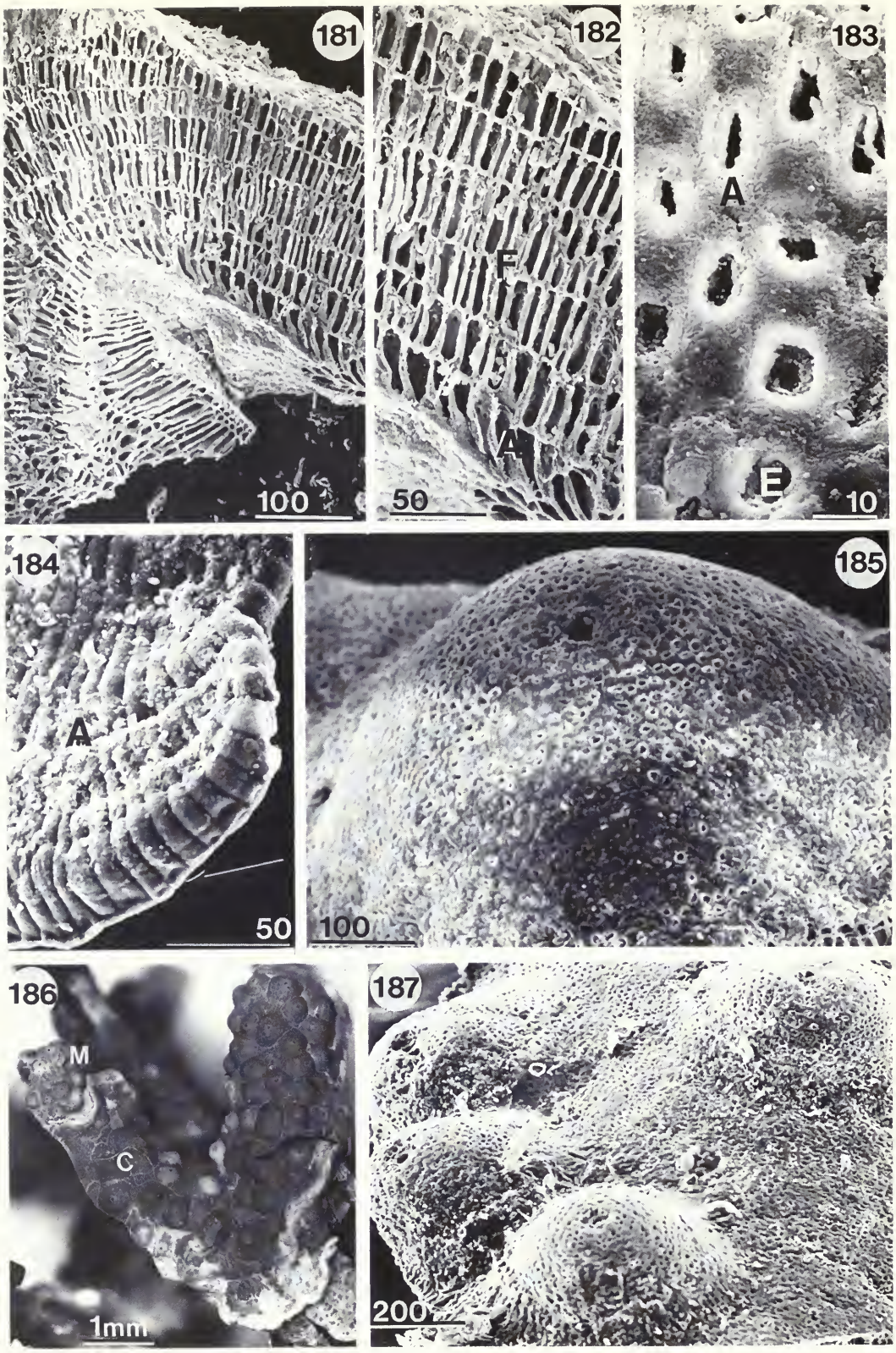
SPERMATANGIAL PLANTS. The only spermatangial plant that has been found was that described in the type material (Figs 158, 167, 197).

CARPOGONIAL/CARPOSPORANGIAL PLANTS. A few carpogonial conceptacles were observed by Rosenvinge (1917) and Suneson (1943) observed one on an otherwise bisporangial crust; none have been found in British Isles material.

BISPORANGIAL PLANTS. Bisporangial conceptacles are more consistent in shape and anatomical structure than in many other *Titanoderma* species. Mature conceptacles are conical (Figs 52g, 175) and stages in conceptacle development (Figs 41, 42, 188–190, 195) are similar to those described in var. *pustulatum* (p. 18). In mature conceptacles (Figs 52f–g) the conceptacle chamber is usually flanked by much stretched thallus cells (cf. Suneson, 1943: 451). Roof filaments are usually composed of one tall cell and an epithallial cell peripherally, extending near the ostiole to four cells which vary in length from being all more or less isodiametric (Figs 52f, 190, 203) to having a tall cell beneath the epithallial cell (Figs 52g, 202). Small papillae often develop round the ostiole and sometimes on the under surface of the roof (Fig. 191) and trichocytes may occur (Fig. 191). Occasional plants occur in which the conceptacles are crowded with swollen cells (Fig. 202) attached to both the roof and base, forming paraphysis-like structures. Rosanoff (1866, pl. IV, figs 11–15) noted the same phenomenon in *Melobesia macrocarpa* (now *T. pustulatum* var. *macrocarpum*). A small columella is usually present (Fig. 190). Old conceptacles sometimes become buried in the thallus (Figs 196, 204) but they are usually infilled.

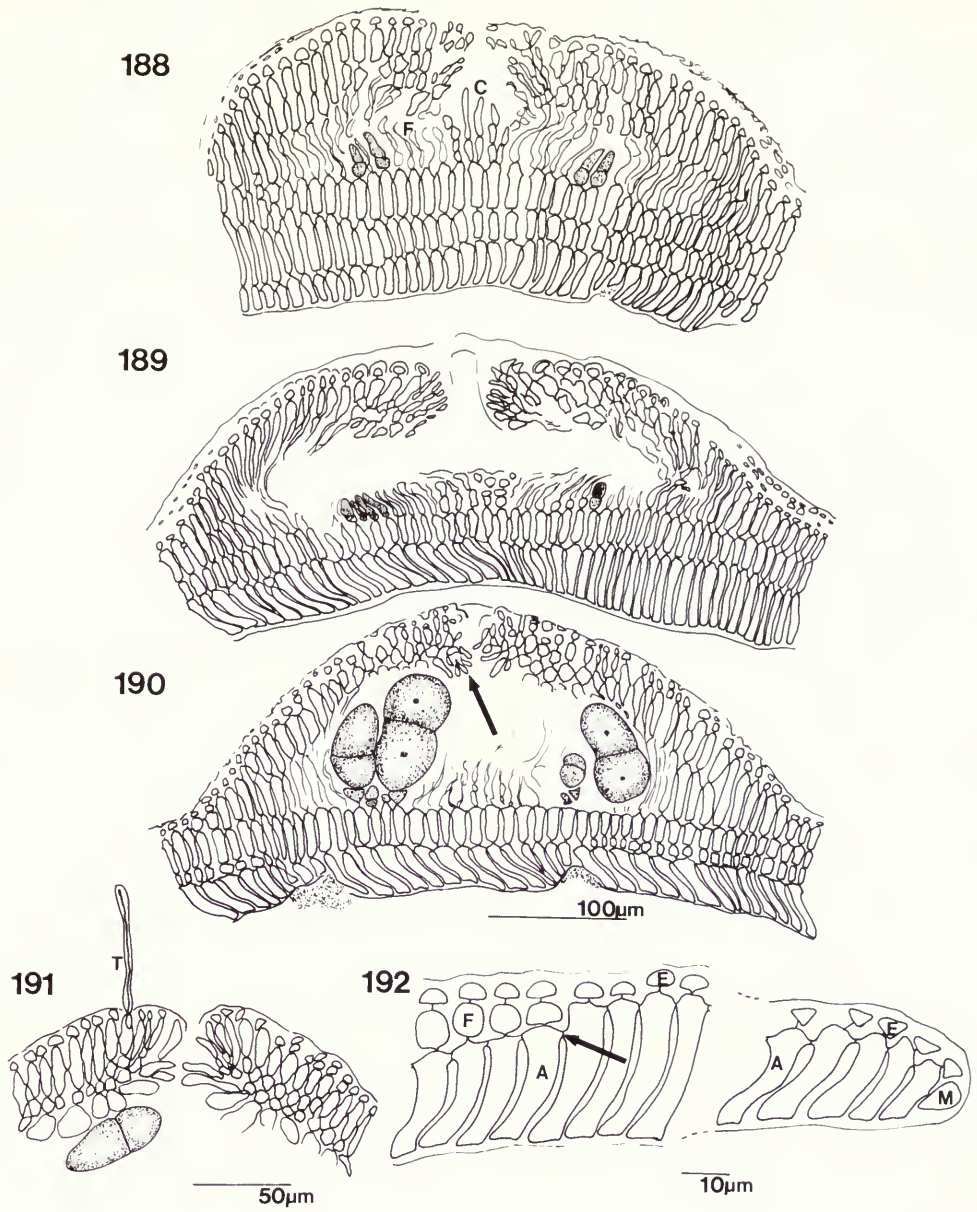
Bisporangia are borne peripherally (Figs 190, 193, 194, 203) on stalk cells, and although they are difficult to count there are possibly up to *c.* 60 per conceptacle. Bisporangia vary in shape from being rather tall, relatively thin, and crescent-shaped (Fig. 52g) to being short and farctate (Figs 52f, 190, 203). Occasional small and possibly stunted tetrasporangia may occur in otherwise bisporangial conceptacles.

VARIATION RANGE. In the British Isles the distinctly blue-toned thalli of var. *confine* growing on *Corallina* and turf algae at low tide level or forming applanate thalli on rocks and shells were initially perceived as true *confine* and the mauver, smoother, thicker-looking plants on *Furcellaria* as *Dermatolithon litorale*. Detailed analysis of cell dimension and reproductive structures showed, however, that no reliable characteristics separated the two entities and they have now been combined. Likewise the apparently pinker, epiphytic plants described by Nichols (1909, as *Lithophyllum macrocarpum* f. *intermedia* and *L. pustulatum* f. *ascripticia*) from



Figs 181–187 Thallus and conceptacle features of *Titanoderma pustulatum* var. *confine* (scales in μm unless stated).

181. Vertical fracture of a 'nodule' of thallus (84/165).
182. Detail of thallus in Fig. 181, showing the tall, lightly calcified axial (A) and erect filament (F) cells.
183. Surface view of thallus margin (83/464) showing axial cells (A) and epithallial concavities (E).
184. Underside of thallus margin (84/399) showing the radiating axial filaments (A); at the growing edge (arrow) a calcified cap curls under to protect the initial.
185. Bisporangial conceptacle (84/399) growing on *Gelidium pusillum*.
186. Plant of minute growth from (M) adjacent to var. *confine* (c) on *Furcellaria* (80/104).
187. General view of bisporangial plant of minute growth form (79/208).



Figs 188–192 Vertical sections of *Titanoderma pustulatum* var. *confine*.

188–190. Stages in the development of a bisporangial conceptacle from Bembridge (84/28B).

188. Bisporangial initials (shaded) on stalk cells still mainly surrounded by remains of erect filament cells (F); central columella (C) retracting to create the ostiole.

189. Cells of erect filaments have now split apart and the roof structure is developing.

190. Mature conceptacle with irregularly shaped roof cells and small papillae (arrow) round the pore.

191. Ostiole (87/62) to show trichocyte (T).

192. Thallus edge (84/28B) to show axial filament initial (M), axial (A) and epithallial (E) cells, and the initiation of erect filaments (F). The primary pit connection (arrow) continues in the axial filament.

California cannot be distinguished anatomically from *T. pustulatum* var. *confine*.

Minute growth form. Analysis of populations of var. *confine* growing on *Furcellaria* at Bembridge (see habitat and phenology, p. 58) showed that a distinct growth form (Fig. 186) occurred there and further examples were later collected in Dorset. This growth form has flat, adherent thalli (Figs 186, 187) up to 400 µm thick, with abruptly emergent, conical bisporangial conceptacles (Fig. 187) which may have a skirt at the base. The conceptacles measure up to 400 µm external diameter and the conceptacle roof is bulbous to stepped when young (Figs 41, 42) and ridged when mature (Figs 44, 187).

The thallus is composed of a single layer of oblique axial cells (Fig. 52h) measuring 14–117 µm high × 8–18 µm diameter, and erect filaments up to four cells long with cells measuring 8–65 µm long × 7–18 µm diameter. Bisporangial conceptacles have more or less hemispherical chambers (Figs 52h, 201) measuring 169–250 µm diameter and 91–130 µm high, the roof is 26–78 µm thick and is up to five cells thick at the ostiole. A small columella is present.

Peripheral bisporangia measure 47–104 μm long x 26–57 μm diameter.

The main difference between this minute growth form and most plants of var. *confine* is the distinctly smaller bisporangial conceptacle (Fig.186) in minute plants. A situation in which gigantic plants arise within a population as a result of polyploidy is a generally recognized phenomenon, and miniaturization, which is also quite a common occurrence, may also have a genetic basis.

In the British Isles the morphological characteristics of individual populations of var. *confine* (e.g. on *Furcellaria* at Bembridge) remain very consistent over periods of years, whereas different populations, even on the same shore, may show distinct differences. This type of variability may be partly a consequence of apomixis, but observations (unpublished) on populations elsewhere which include gametangial and tetrasporangial plants suggest that the situation is much the same. This is a well-recognized phenomenon in animal (e.g. Simpson, 1961: 176) and plant (e.g. Davis & Heywood, 1963) taxonomy and has led to a plethora of infraspecific categories with names depending on whether the variability was considered to be phenotypic or genotypic. Davis & Heywood (1963: 404) give sound advice regarding such categories: 'They should not be given formal latin names ... but their range of variation should be included in the description of the taxon which produces them and even specifically mentioned'. This referred to the use of 'phenecotypes' but is a useful general guideline and is applied to the taxa in this investigation.

Plants of the minute growth form are similar to *T. pustulatum* var. *canellatum* and the relationship and possible differentiation between these two entities is discussed on p. 64.

DISTRIBUTION. *British Isles*: Shetland, Sutherland, Northumberland, Yorkshire, Hampshire, Dorset, Devon, Cornwall, Jersey, Dyfed, Anglesey, Isle of Man, Mull, Co.Clare, Co.Galway, Co.Down. [The minute growth form has been collected in Hampshire and Dorset]. *World*: Confirmed from Denmark, Sweden, northern and western France, Mediterranean, India, California, South Africa and southern Australia. [Some records from the Mediterranean (e.g. Hamel & Lemoine, 1953; van der Ben, 1969; Cormaci & Furnari, 1979, as *Dermatolithon litorale*) may refer to *T. pustulatum* var. *canellatum*].

HABITAT AND PHENOLOGY. *Titanoderma pustulatum* var. *confine* is mainly epiphytic, growing intertidally on a range of algal hosts; it has also been recorded as growing on rocks subtidally to a depth of 45 m (Adey & Adey, 1973, fig. 58), but I have not been able to confirm this record. I have found plants growing directly on rocks at low tide level and others that were growing on fragments of old crustose corallines such as *Phymatolithon lenormandii*. A number of intertidal populations of var. *confine* in the British Isles have been sampled sequentially and some preliminary observations published (Chamberlain, 1978*a*, as *Dermatolithon litorale*). An updated summary of the results of sequential sampling are as follows:

Bembridge, Isle of Wight

Bembridge (Fig. 49) is a fairly sheltered, gently sloping, NE.-facing, limestone shore comprising a series of lagoons and low-tide runs which do not dry out even at low tide, and an expansive seaward ledge or platform that has many shallow pools on its surface.

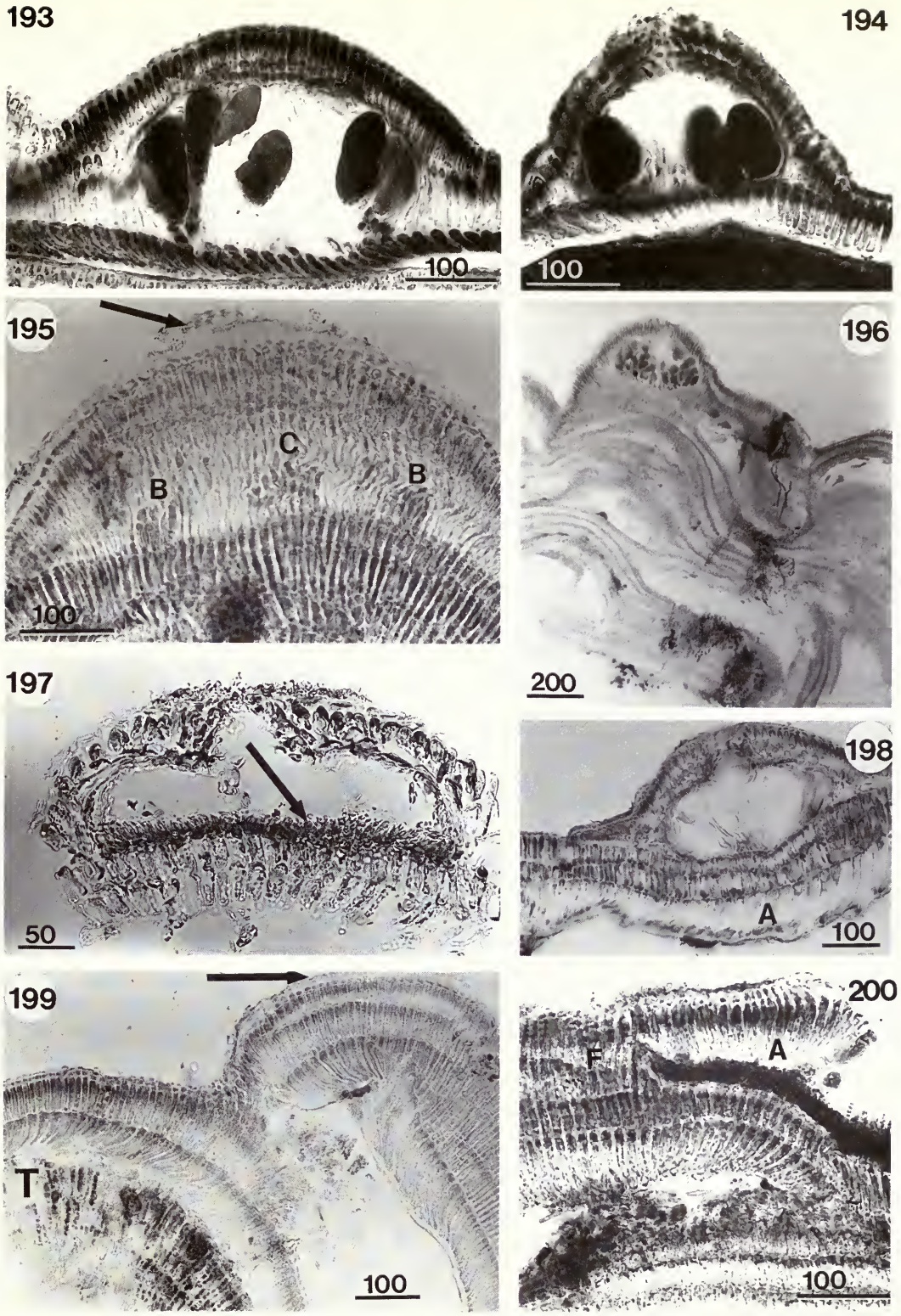
In one of the low tide runs *Cystoseira nodicaulis* was common in the mid 1970's (Chamberlain, 1978*a*: 399) when it bore plants of *Fosliella farinosa* on its basal tophules all year round, and var. *confine* sporadically, usually on branches but occasionally on basal tophules. Observations between October 1975 and December 1977 showed var. *confine* to be particularly abundant in October 1975, February 1976, and July 1977 which shows no detectable pattern of seasonal occurrence. During the 1980s the host plant disappeared from this lagoon.

Another, more abundant population of var. *confine* occurs on many algal hosts in shallow pools on the seaward ledge; the hosts include *Corallina officinalis, Halopitys incurvus, Gelidium pusillum, Laurencia pinnatifida, Sargassum muticum* (Yendo) Fensholt, and *Cladophora rupestris*. These algae are frequently covered with a mass of var. *confine* (Figs 169, 170, 186), including the minute growth form, and *T. corallinae*; other common, small, crustose epiphytes include *Melobesia membrancea, Fosliella farinosa, Pneophyllum limitatum*, and *P. microspsorum* (Rosenvinge) Y.Chamberlain. The host algae may be eaten by *Littorina* and *Furcellaria* in particular is often cropped to water level, the gasteropods apparently consuming coralline crusts together with the host plants. Samples of host plants were collected monthly from November 1978 to February 1980 and observed qualitatively. The principal features of note were that all host plants were smothered with tiny *Titanoderma* sporelings in July 1979 and these had grown to young more or less discoid plants by August. Mature plants of var. *confine* were most abundant and in good condition in November 1978 and 1979, and January, May, and September 1979. Plants were in poor condition, with the conceptacles becoming buried by thallus growth, after spells of cold weather in February 1979 and 1980 and remained poor in March and April 1979. Whatever the condition of var. *confine* plants, at least some conceptacles were present in all collections. The minute growth form (Fig. 186) and also *T. corallinae* (Fig. 170) were present on all occasions but were most prevalent from June to August 1979.

Kimmeridge, Dorset

Kimmeridge (Fig. 49) is a very sheltered, south-facing bay with a shore composed of soft, oil-bearing shale transected at intervals by hard, greensand ridges running from the upper shore into the subtidal. The largest, centrally situated ledge was studied in most detail (Chamberlain, 1978*a*) and has two habitats of particular interest, shallow pools on the upper surface and a *Laurencia pinnatifida* band at mid tide level on the steep, west-facing edge. The *Laurencia* band is associated with a basal turf of algae such as *Gelidium pusillum, Lomentaria articulata* (Hudson) Lyngbye, *Corallina officinalis*, and *Cladophora pellucida* (Hudson) Kütz. Sometimes *Laurencia* plants are very small and form part of the turf, at other seasons they grow to about 70 cm tall and project well beyond the turf. Sequential samples were taken from the *Laurencia*/turf population in August 1976 and at two monthly intervals from November 1976 to January 1980. During this time it was found that var. *confine*, together with its minute growth form, occurred on the basal turf on most occasions but was particularly abundant in July 1977, July, September, and November 1978, July 1979, and January and July 1980, while it occurred more rarely on *Laurencia* fronds although it was noted particularly in August 1976 and July 1979.

Many algae occur in the pools on top of the ledge, but *Halopitys incurvus* and *Corallina officinalis* are two of the



Figs 193–200 Vertical sections of *Titanoderma pustulatum* var. *confine* (scales in μm).

193. Bisporangial conceptacle from plant growing on *Lomentaria articulata* in Dorset (87/62).
194. Bisporangial conceptacle of minute growth form on *Laurencia pinnatifida* in Dorset (87/62).
195. Young bisporangial conceptacle from plant growing on *Furcellaria lumbricalis* at Bembridge (86/63). Bisporangial initials (B), and columella initials (C) can be seen among stretched cells. Epithallial cells (arrow) are being shed.
196. A bisporangial conceptacle and a series of regenerating thalli growing on a limpet at Portrush, Northern Ireland (86/1).
197. Spermatangial conceptacle from the lectotype of *Melobesia confinis* (Figs 158, 167), short attached spermatangia (arrow) grow on the conceptacle floor.
198. Bisporangial conceptacle from plant (83/340) growing on *Littorina* at Bembridge. Note the characteristically tall, sinuate axial cells (A).
199. Interweaving thalli (84/152) that have regenerated from senescent thallus (T). Epithallial shedding (arrow) is occurring.
200. Regeneration of an axial filament (A) from subepithallial initials (F) (84/141).

most common species and in March 1977 these and all other algae in such pools were covered with var. *confine*.

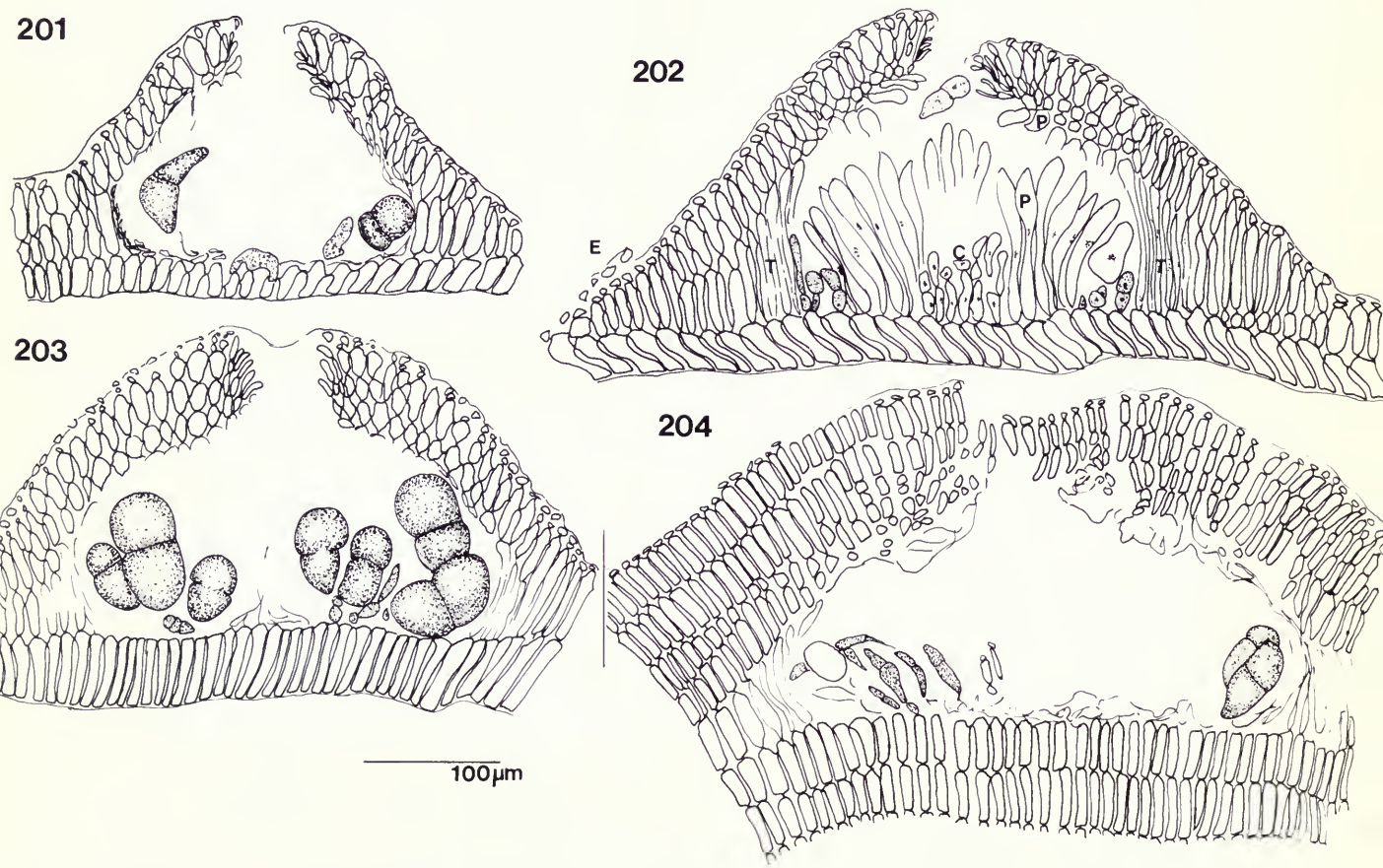
Port Cornaa, Isle of Man

Port Cornaa is an east-facing shore on the Isle of Man (Fig. 49). Var. *confine* (Fig. 172) occurs there as an epiphyte on *Corallina officinalis* growing in the outlet of a rock pool at about mean high water neap tide level. I am much indebted to Mr Tom Whipp who sampled this population at two monthly intervals from March 1984 to January 1985. In March 1984 the plants were in good condition but not fertile, in May they were rather poor, but fertile plants were present in July and September. The mainly bisporangial conceptacles contained a few tetrasporangia among the bisporangia on each occasion. In October 1984 and January 1985 non-fertile plants were again present.

Considering the populations studied at the three above localities, it would seem that on the whole var. *confine* is most abundantly fertile in summer, particularly in July. This conforms to Chihara's (1974*a*: 266, as *Dermatolithon*) results in finding *Titanoderma* reproducing mainly in summer in Japan and Suneson's (1943: 39, as *L. litorale*) observations in Sweden. However, occurrence of *Titanoderma* may also be very sporadic and show no perceptible pattern of growth or reproduction, as was found by Goss-Custard et al. (1979) at Lough Ine, SW. Ireland, when they studied the occurrence of *T. corallinae* (as *Dermatolithon*) on *Corallina*. It seems that populations may be maintained at low levels on associations such as algal turfs, from which they are able to populate other substrata very rapidly when favourable conditions develop. Although var. *confine* is mainly summer fertile, conceptacles are present on most of the samples studied. It is possible that at other times the spores are not very viable, a phenomenon quite frequently observed in coralline algae; Jones & Woelkerling (1983), for example, found that *Fosliella cruciata* produced tetrasporangial conceptacles all year round in Australia, but only the spores from plants collected in April and June (autumn) germinated in the laboratory, and Chamberlain (1987) observed that the spores of *Pneophyllum* plants grown in the laboratory germinated more readily in autumn although conceptacles were present throughout the year.

Rockall (350 km west of Scotland).

Epilithic plants of *Titanoderma* were collected from this exceedingly exposed rock by Keith Hiscock and Sue Hiscock (e.g. Y.M.C. 88/132). They show extensively imbricating thalli with tall, thin cells and almost



Figs 201–204 Vertical sections of bisporangial conceptacles of *Titanoderma pustulatum* var. *confine*.

201. Lectotype of *Lithophyllum pustulatum* f. *intermedia* Foslie (see Fig. 164).

202. Immature conceptacle growing on *Lomentaria articulata* (87/62) with paraphysis-like cells (P), young bisporangial initials (shaded), and central columella cells (C). Tall erect filament cells (T) are present at the periphery. and final remains of old epithallial cells are being shed (E).

203. Conceptacle from Rhoscolyn (78/329) growing on *F. lumbricalis*, with a thick roof of more or less equal-sized cells. This material has stepped roof cells (Fig. 180).

204. Old conceptacle of an epilithic plant (84/416) that is becoming immersed by thallus growth, abortive bisporangia remain in the conceptacle.

certainly pertain to var. *confine*. However, conceptacles were in too poor condition for final confirmation (cf. p. 36).

HERBARIUM SPECIMENS CONFIRMED AS T. PUSTULATUM VAR. CONFINE. As *Melobesia confinis, Le Jolis*, Alg.mar.Cherbourg 275 (herbarium no. 2365) (BM!, CHE!, PC!) (Figs 159–163, 166); as *Dermatolithon* (*Melobesia*) *hapalidioides* f. *confinis*, British Isles, Co.Mayo, Clew Bay, Roonagh Quay, on limpets, 15 February 1911, *A. D. Cotton*, det. Mme P. Lemoine (BM Box 919!) (Fig. 174); British Isles, Devon, Torquay, on *Corallina officinalis*, March 1892, *E. M. Holmes* (BM!); British Isles, Northumberland, Berwick, on *C. officinalis*, October 1884 & 29 January 1887, *E. A. Batters* (BM!); as *Dermatolithon hapalidioides*, British Isles, Yorkshire, Robin Hood's Bay, on a shell, August 1901, *E. M. Holmes*, Alg.Br.mar.Exsicc.Fasc.XI, 254 (BM!); as *Lithophyllum macrocarpum* f. *intermedium*, U.S.A., California, La Jolla, on various hosts, *M. B. Nichols*, nos 396, 415, 417, 535 & 596 (UC!); Denmark, Limfjorden, on *Fucus vesiculosus*, 28 June 1906, *L. K. Rosenvinge* 8055 (LD! TRH!); as *Lithophyllum macrocarpum*, Denmark, Nordre Rönner, on *Fucus*, 27 September 1894, *L. K. Rosenvinge* 5350 (C!); and many further Rosenvinge specimens (C!); as *Lithophyllum litorale*, Sweden, Kristineberg, outside Blåbergsholmen, 0.5–1 m depth, on *Fucus vesiculosus*, 13 August 1947, *S. Suneson* (LD! and Suneson's personal collection!); as *Dermatolithon ascripticium*, U.S.A., California, on various hosts, *M. B. Nichols*, nos 398, 423, 432, 528 & 609 (UC!). British Isles specimens in herb. *Chamberlain*: Anglesey, Rhoscolyn, on *Furcellaria lumbricalis*, intertidal, 1 December 1978, 78/329; Hampshire, Isle of Wight, Bembridge, the ledges, on *Furcellaria*, 27 June 1979, 79/208; Dorset, Kimmeridge, on *Halopitys incurvus*, *Corallina officinalis, Furcellaria* and *Gelidium pusillum*, intertidal, 20 January 1980, 80/9–12; Dorset, Kimmeridge, on *Laurencia pinnatifida*, intertidal, 13 July 1980, 80/66; Hampshire, Isle of Wight, Bembridge, the ledges, on *Furcellaria* and *Cladophora rupestris*, intertidal, 24 September 1980, 80/105, 80/107; Hampshire, Isle of Wight, Bembridge, the slipway, on *Littorina*, intertidal, 6 October 1983, 83/340; Hampshire, Isle of Wight, Bembridge, upper channels, on *Ostrea*, 2 December 1983, 83/464; Isle of Man, Scarlett Point, on rocks at low tide, 17 March 1984, 84/141; Isle of Man, Port Cornaa, on rocks and *Corallina*, mid tide, March 1984 and October 1984, 84/165 and 84/399; Dyfed, West Angle, on rock in pool, 10 December 1984, 84/416; Dorset, Kimmeridge, on *Palmaria palmata*, intertidal, 17 October 1986, 86/135A; Dorset, Chapman's Pool, 30 July 1987, 87/62, on *Laurencia pinnatifida, Lomentaria articulata* and *Gelidium pusillum* turf, intertidal, 30 July 1987, 87/62; Hampshire, Isle of Wight, Freshwater, on *Fucus serratus* and *Palmaria*, intertidal, 20 September 1987, 87/68; Rockall, east side, on rock, 2 m above low tide, 29 June 1988, 88/123. Minute growth form; 79/208, 80/9, 87/62 (see above).

HERBARIUM SPECIMEN MISIDENTIFIED AS T. PUSTULATUM VAR. CONFINE. As *Lithophyllum pustulatum* f. *intermedia*, Sweden, Kristineberg, on *Zostera*, 22 August 1905, *H. Kylin* (TRH!, LD!). (= *Fosliella cruciata* Bressan)

1d. **Titanoderma pustulatum** var. **canellatum** (Kütz.) Y. Chamberlain, **comb.nov.**—*Melobesia pustulata* β *canellata* Kütz., *Spec. alg.*: 696 (1849). Type: M. mediterran, In ceramio, specimen 940.317.503 (L!—lectotype selected here)

NOTE. The epithet *canellatum* has priority at varietal rank over *verrucatum* Lamouroux—see Art. 60 of Greuter (1988). Figs 52i, 205–207.

Melobesia verrucata Lamouroux, *Hist. polyp. coralL*: 316 (1816).—*Titanoderma verrucatum* (Lamouroux) Y. Chamberlain in *Cryptogamie: Algol.* **7**: 201 (1986). Type: Mediterranean, on *Rytiphlaea*, *Lamouroux* (CN!—holotype, see Chamberlain in *Cryptogamie: Algol.* **7**: 201, 1986).

ILLUSTRATIONS. As *Dermatolithon litorale*, Chamberlain in *Br.phycol.J.* **17**: figs 3 and 7 only; Garbary, *In* D. E. G. Irvine & J. H Price (Eds), *Modern approaches to the taxonomy of red and brown algae*: fig.17 (1978); as *Titanoderma verrucatum*, Chamberlain in *Cryptogamie: Algol.* **7**: figs 4–10 (1986).

DESCRIPTION. Plants epiphytic, adherent, flat, to 3 mm diameter, 90 μm thick, adjoining plants not overgrowing one another, pinkish, greyish or violet, surface smooth. Single layer of *axial filaments* with cells obliquely orientated and sinuate, cells 33–91 μm high × 6–7 μm diameter, cytoplasmic contents mainly at tops of cells, *erect filaments* absent except in immediate vicinity of conceptacles, *epithallial cells* triangular, *trichocytes* occasional. *Gametangial and tetrasporangial plants* not seen; *bisporangial conceptacles* very prominent, rounded, arising abruptly from thallus surface, often with a skirt at the base, 250–400 μm external diameter, conceptacle surface regularly stepped, conceptacle chamber hemispherical, 130–350 μm diameter, 68–215 μm high, roof 26–52 μm thick, roof three cell layers thick throughout, epithallial and inner cells small, middle cell taller, somewhat clavate, and usually lengthening to increase roof thickness at ostiole, small papillae sometimes lining the ostiole, columella slightly- to well-developed, *bisporangia* 60–75 μm long × 28–36 μm diameter.

HISTORICAL. For the sake of completeness, the following (emended) discussion from Chamberlain (1986) is repeated:

'The original publication of *Melobesia verrucata* (Lamouroux, 1812: 186) was a nomen nudum, but Lamouroux (1816) later published a brief description of the species which he thought was a polyporous animal. Since 1816 the concept of *M. verrucata* has undergone many vicissitudes. Until now, however, the type specimen has not been re-examined nor have most of the specimens on which subsequent records were based.

'Following Lamouroux, Harvey (1849, 1851, pl.347C) recorded and figured plants growing on *Phyllophora* in Ireland as *M. verrucata*, but Harvey's specimens cannot be found and his description, while almost certainly representing *Titanoderma*, does not enable identification of his material. Areschoug (1852: 513) retained *M. verrucata* Lamouroux, adding Harvey's record and also Kützing's (1849: 696, 1869: 34, tab. 96). However, examination of Kützing's specimen (L 940.317.498!) shows it to be a foraminiferan, although the specimens of *M. pustulata* β *canellata* Kützing (1849: 696) are true *M. verrucata* (L 904.315.502! and 940.317.530!).

'The superficial resemblance of *M. verrucata*, with its delicate thallus and prominent conceptacles to *Fosliella* spp. (subfamily Mastophoroideae), led the Crouan brothers (1860, 1867) to identify as *M. verrucata* plants of *Fosliella farinosa* (Lamouroux) Howe growing on *Phyllophora* (CO!), and a mixture of *F. farinosa* and *Pneophyllum limitatum* (Foslie) Y. Chamberlain growing on *Fucus serratus* L. (CO!). The *Phyllophora* epiphyte led to *M. verrucata* occurring in the synonymy of *M. farinosa* (Foslie, 1900*a*, 1900*b*, 1905*a*; Hamel & Lemoine, 1953) while the *Fucus* epiphyte was

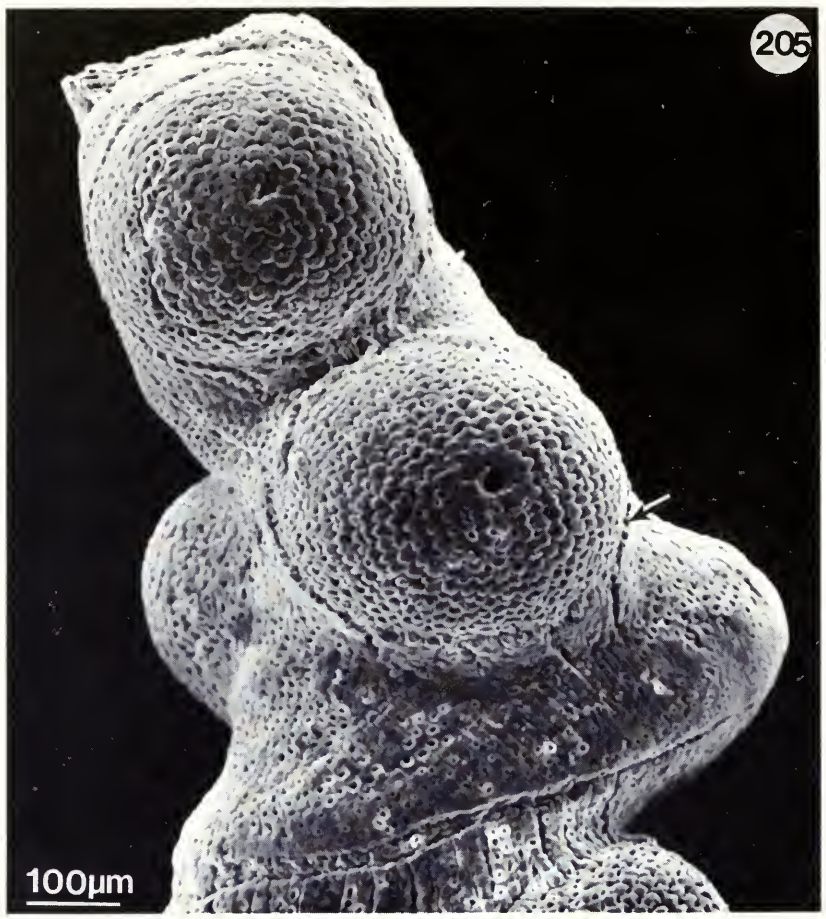


Fig. 205 *Titanoderma pustulatum* var. *canellatum* (78/142) growing on *Cladophora rupestris* from Kimmeridge, showing the stepped roof and skirt round the base (arrow) of the conceptacle.

subsequently presumed to be *Dermatolithon pustulatum* (Foslie, 1900*a*, 1905*a*; Hamel & Lemoine, 1953).

'Le Jolis (1863: 151) transferred *M. verrucata* to *M. membranacea* (Esper) Lamouroux, probably because Harvey himself remarked that the plants resembled old thalli of *M. membranacea*. Rosanoff (1866: 66), also included Harvey's *M. verrucata* in *M. membranacea* although he thought (Rosanoff, 1866: 69) that *M. verrucata* was '*Melob. pustulata* croissant sur un *Rhytiphloea*'. Furthermore he appended a note to Lamouroux's type concluding that the specimens were stages of the development of "la pustulosa". Further evidence that Rosanoff considered *M. verrucata* and *M. pustulata* to be conspecific occurs in a note from Le Jolis to Johnson & Hensman (1899: 26): "(*M. verrucata*, Lmx.). I do not possess any specimens of the enigmatic *M. verrucata* Lamx.; and my opinion is that such a name should be suppressed. Rosanoff, a very clever and conscientious botanist, who, at my request, undertook here the study of Melobesieae, went to Caen in order to investigate the type specimens of Lamouroux's herbarium, and ascertained that the specimen labelled *M. verrucata* by Lamouroux is nothing but *M. pustulata*'.

'An examination of many of the specimens at CHE cited under *M. pustulata* by Rosanoff (1866: 74) shows that, for the most part, they are true *Titanoderma pustulatum* var. *canellatum*, although the following taxa are also represented: *Fosliella* spp., *T. pustulatum* var. *pustulatum* and *Pneophyllum limitatum*. Finally, Rosanoff (1866: 73) cites '*M. canellata*' by Kützing (1849) as being true *M. pustulata*. Many subsequent authors have followed the practice of subsuming *M. verrucata* in *M. pustulata* including De Toni (1905: 1771, pro parte—as *Dermatolithon*), Hamel & Lemoine (1953: 59, pro parte—as *Dermatolithon*) and Foslie (1905*a*: 118—as *Lithophyllum*).

'As a result of the conflicting ideas outlined above, it is evident that the concept of a small taxon of *Titanoderma* corresponding to Lamouroux's *Melobesia verrucata* virtually ceased to be recognized in the early years of this century. More recently, however, a number of authors (e.g. Hamel & Lemoine, 1953; Dawson, 1955; Kylin, 1956; van der Ben, 1969; Lemoine, 1971; Parke & Dixon, 1976; Chamberlain, 1978*a*, 1978*b*; Garbary, 1978; Cormaci & Furnari, 1979; Cormaci, Furnari & Scammacca, 1979; Battiato et al., 1982; Suneson, 1982) have recorded, as *Dermatolithon litorale* (Suneson) Hamel & Lemoine, small plants of *Titanoderma* from the Mediterranean and northern Europe. Suneson (1943, as *Lithophyllum*) based *D. litorale* on *Lithophyllum pustulatum* f. *intermedia* Foslie (1905*a*: 117) and examination of both Foslie's (TRH! and C!) and Suneson's (LD! and personal herbarium!) material shows this species (now subsumed in *T. pustulatum* var. *confine* q.v.) to be distinct from var. *canellatum*. With regard to the above references, Hamel & Lemoine (1953), Dawson (1955), Kylin (1956), and Lemoine (1971) base their records on Suneson's (1943) description and are presumably not, therefore, referring to var. *canellatum*. The references for the Britsh Isles by Parke

& Dixon (1976), Chamberlain (1978*a*), and Garbary (1978) should however, be re-named var. *canellatum* while the extended description (Chamberlain, 1978*b*) relates to a mixture of var. *canellatum* and var. *confine*. Finally, it is probable that the other authors mentioned above are sometimes using the name *litorale* for the ubiquitous plant now known as *T. pustulatum* var. *canellatum*.

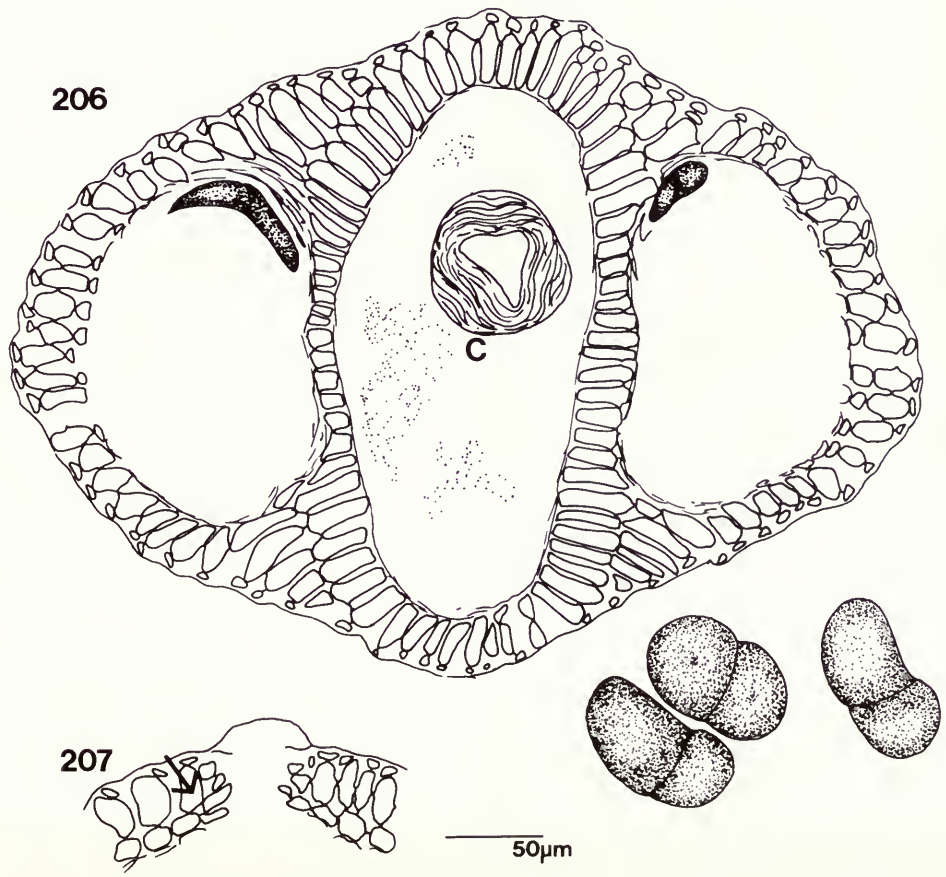
'To summarize, therefore, the delicate plants with small, prominent conceptacles which characterize var. *canellatum* have been collected extensively throughout Europe but have been confused with other taxa, in particular *Fosliella* spp., *Pneophyllum limitatum*, and other species of *Titanoderma*. This is understandable because the external morphology is very similar in all these entities, but the characteristically oblique, sinuate axial filament cells of var. *canellatum* instantly distinguish this taxon from members of the other genera, while no other *Titanoderma* has been described to date with conceptacles as small and prominent as var. *canellatum*. A note should be made regarding Lamouroux's unpublished species *Melobesia discoidea*. A number of specimens in Caen (!) have been labelled Melobesia Discoidea by Lamouroux; they mainly refer to calcareous epiphytes on *Padina* comprising a mixture of *Fosliella* spp. and *T. pustulatum* var. *canellatum*. Rosanoff (1866: 70) refers to *M. discoidea* in his discussion of *Melobesia farinosa*, of which species he considered it to be a robust form and he also refers to it in his annotations on Lamouroux's specimens (CN!). As the name was never published it is of no further concern, but it clearly referred to a small, epiphytic entity with prominent conceptacles which included var. *canellatum*.'

In the British Isles, Batters (1902: 97) recorded *Melobesia verrucata* as a synonym of *Dermatolithon pustulatum*. According to the specimens in BM that were probably the basis of Batters's record (see herbarium specimens misidentified as *T. pustulatum* var. *canellatum*), this name was applied to plants with small, prominent conceptacles attributable to var. *confinis* or *Pneophyllum* spp.

PLANT APPEARANCE. *Titanoderma pustulatum* var. *canellatum* forms small, thin, pinkish, greyish or violet thalli on *Cladophora* (Fig. 205), *Jania,* and *Gelidium*, and it has prominent conceptacles usually with a distinct 'skirt' (Fig. 205) between conceptacle and thallus surface. The conceptacle has a stepped roof surface and the thallus surface is composed of elongated axial cells with short epithallial concavities (Fig. 205).

VEGETATIVE ANATOMY. The bistratose thallus (Fig. 206) is composed of relatively tall, oblique axial cells and small, more or less triangular epithallial cells.

BISPORANGIAL PLANTS. Bisporangial conceptacles (Fig. 206) are prominent and may have an almost globular conceptacle chamber (Figs 52i, 206) when growing on filamentous algae such as *Cladophora*. The roof is usually three cells thick with the central cell being tallest (Figs 52i, 206). More or less ovate bisporangia (Fig. 206) are borne peripherally; columella remnants may occur centrally.



Figs 206–207 Vertical sections of *Titanoderma pustulatum* var. *canellatum*.

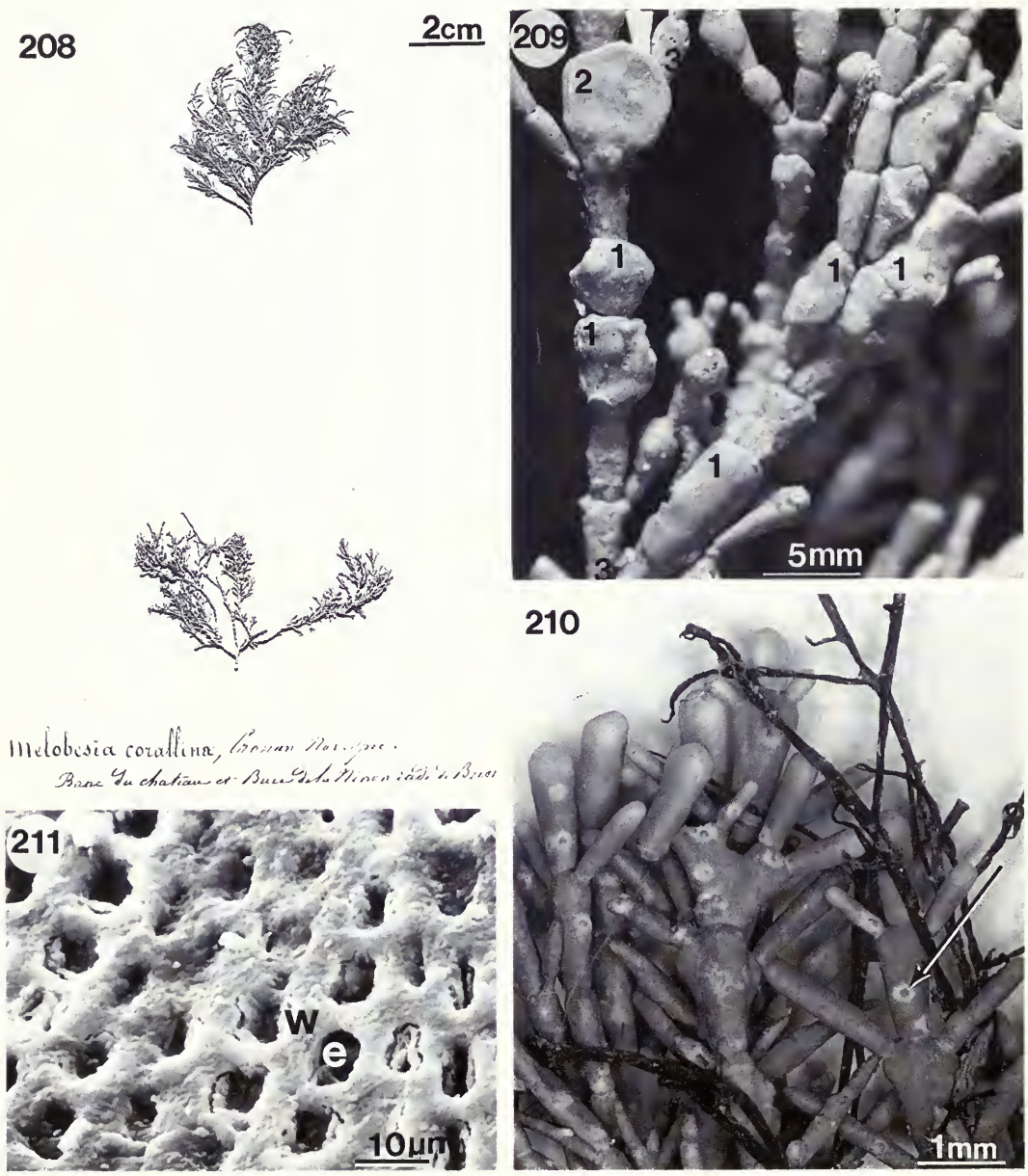
206. Plant with two bisporangial conceptacles (80/107B) completely encircling a filament of *Cladophora rupestris* (C) and accumulated débris, three bisporangia have been extruded.

207. Ostiole of bisporangial conceptacle (78/142) showing the clavate central cell of the roof (arrow).

DISTRIBUTION. *British Isles*: Hampshire, Dorset, Jersey, Co.Cork. *World:* Mediterranean (including the Aegean and Adriatic Seas)

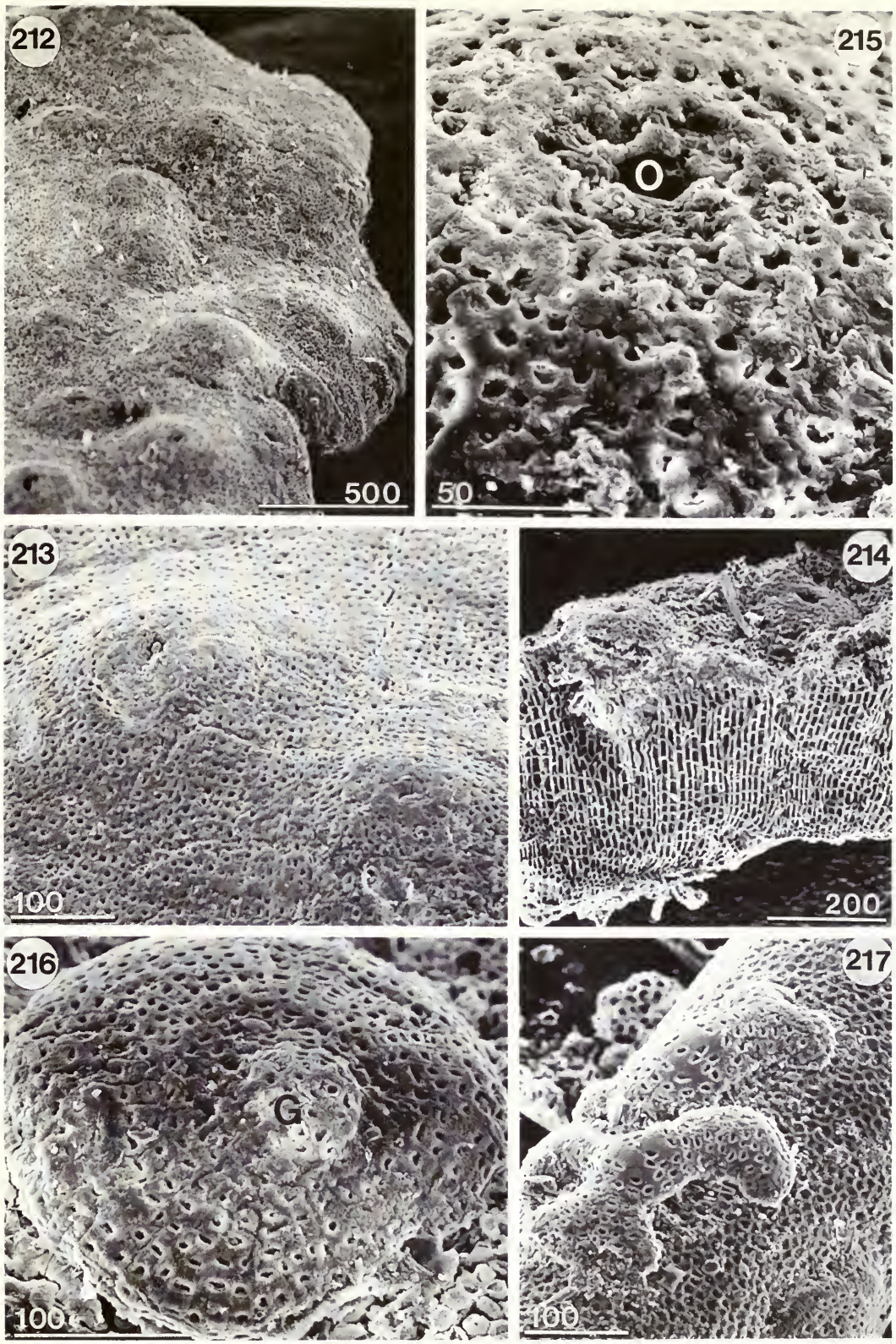
HABITAT AND PHENOLOGY. Forming small thalli on turf algae such as *Cladophora pellucida, C. rupestris, Jania rubens* (L.) Lamouroux, and *Gelidium pusillum* collected in intertidal pools. Bisporangial plants collected in May, August, and September.

TAXONOMIC NOTE. *Titanoderma pustulatum* var. *canellatum* appears to be a common plant in the Mediterranean, Aegean and Adriatic Seas, growing epiphytically on a wide range of algal and seagrass hosts. It was previously supposed (Chamberlain, 1978*a*, as *Dermatolithon litorale*) that it occurred quite frequently in the British Isles, particularly on algal hosts in southern England and western Ireland. During this investigation, however, in-depth analysis of populations of *T. pustulatum* var. *confine* at Kimmeridge and Bembridge has shown the presence of a minute growth form of this variety (see p. 58) and most of the plants previously attributed to *D. litorale* belong either to var. *confine* or its minute growth form. Plants now included in var. *canellatum* are differentiated by the complete absence of erect filaments, the presence (in VS) of a consistently three-celled bisporangial conceptacle roof, and a regularly stepped conceptacle surface. Plants attributed to the minute growth form of var. *confine*



Figs 208–211 *Melobesia corallinae*.

208. Lectotype specimen (CO).
209. Sleeve-like (1) and discoid (2) plants growing on *Corallina* (78/305). Damaged surfaces (3) remain after the epiphyte has fallen off.
210. Sporelings (arrow) settling on adaxial surface of *Corallina* causing bleaching of its thallus as they develop (78/305).
211. Thallus surface showing heavily calcified cell walls (w) surrounding slightly elongated epithallial concavities (e) (78/305).



Figs 212–217 Scanning electron micrographs of *Titanoderma corallinae* (scales in μm).

212. Bisporangial plant (79/208) with slightly raised conceptacles.
213. Bisporangial plant (78/305) showing two conceptacles and the thallus cells arranged in radiating rows as in Fig. 216.
214. Vertical fracture of plant (78/305) showing the thick thallus with non-aligned cells. Two conceptacles are seen in surface view.
215. Ostiole (o) and roof of bisporangial conceptacle (79/208) showing the haphazard arrangement of roof cells.
216. Discoid sporeling (78/305) growing on *Corallina*. The remnants of the original germination disc(s) (cf. Fig. 3) apparently remain on the surface. Note radiating thallus filaments.
217. Two branching sporelings (78/305) growing on *Corallina*, it is possible that this form arises from adjacent settlement of two bispores from a sporangium.

usually have some development of erect filaments, the conceptacle roof (in VS) is variably constructed but is not usually consistently three cells thick, and the conceptacle surface is irregularly ridged or stepped. However, further investigation, particularly of Mediterranean populations, is needed to assess the relationship between these two taxa. It seems possible that var. *canellatum* originated as a miniature growth form of var. *confine* and has become particularly widely established in the warm waters of the Mediterranean.

HERBARIUM SPECIMENS CONFIRMED AS T. PUSTULATUM VAR. CANELLATUM. As *Melobesia pustulata* β *canellata, Kützing* (L 904.315.502!); *Kützing* (L 940.317.503!-lectotype); British Isles specimens in herb. *Chamberlain*: Co.Clare, Carrickadda, on *Cladophora rupestris*, intertidal, 27 August 1976, 76/193; Dorset, Kimmeridge, on *Cladophora pellucida*, intertidal, 25 May 1978, 78/142.

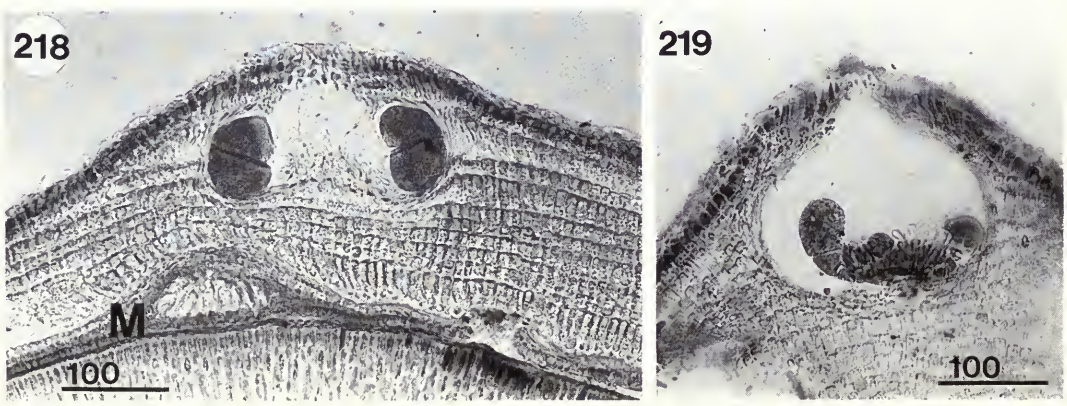
HERBARIUM SPECIMENS MISIDENTIFIED AS T. PUSTULATUM VAR. CANELLATUM. As *Melobesia verrucata*, Mediterranean, ad Algas, *Kützing* (L 940.317.498!) (= a foraminferan); France, Banc du Moulin Blanc, on *Fucus serratus*, February 1859, *P.-L. & H.-M. Crouan* (CO!) (= a mixture of *Fosliella farinosa* and *Pneophyllum limitatum*); France, anse du Minon, on *Phyllophora rubens*, March 1847, *P.-L. & H.-M. Crouan* (CO!) (= *Fosliella farinosa);* British Isles, Northumberland, Berwick, on *Corallina* with *Titanoderma corallinae*, October 1884, *E. A. Batters* (BM!) (=var. *confine*); British Isles, Sussex, Brighton, on *Palmaria, M. P. Merrifield* (BM!) (= *Pneophyllum* spp.); Cornwall, Fowey, 14 November 1882, on red alga, *T. H. Buffham* (BM!) (= *Pneophyllum limitatum).*

2. **Titanoderma corallinae** (P. & H. Crouan) Woelkerling, Y. Chamberlain & P. Silva in *Phycologia* **24**: 333 (1985).—*Melobesia corallinae* P. & H. Crouan, *Fl. Finistère*: 150 (1867).—*Lithophyllum corallinae* (P. & H. Crouan) Heydrich in *Ber.dt.bot.Ges.* **15**: 47 (1897).—*Dermatolithon corallinae* (P. & H. Crouan) Foslie in Børgesen, *Mar.alg. Faeröes*: 402 (1902).—*Lithophyllum pustulatum* f. *corallinae* (P. & H. Crouan) Foslie in *K.nor. Vidensk. Selsk.Skr.* **1905**(3): 118 & 127 (1905).—*Lithophyllum macrocarpum* f. *corallinae* (P. & H. Crouan) Foslie in *K.nor. Vidensk. Selsk.Skr.* **1909**(2): 47 (1909).—*Tenarea corallinae* (P. & H. Crouan) Notoya in *Bull.Jap.Soc.Phycol.* **22**: 47–51 (1974), invalid (Art. 33.2). Type: France, Rade de Brest, Banc du Chateau et Baie de la Ninon, *P.-L. & H.-M. Crouan* (CO!—lectotype selected here) (Figs 208, 220, 221).

Figs 52j, 208–224.

ILLUSTRATIONS. As *Melobesia corallinae*, P. & H. Crouan, *Fl.Finistère*: pl.23, 133 bis, figs 6–11 (1867); as *Lithophyllum corallinae*, Rosenvinge in *K.dansk. Vidensk.Selsk.Skr.* II, **7**: figs 186–190 (1917); Suneson in *Acta Univ.lund.* II, **39**: figs 24–26, pl.6, fig.28, pl.8, fig.38 (1943); as *Dermatolithon corallinae*, Masaki & Tokida in *Bull.Fac.Fish.Hokkaido Univ.* **10**: pl.1, figs 1–4, pls 2, 4, 5 (1960); Garbary *in* D. E. G. Irvine & J. H. Price (Eds), *Modern approaches to the taxonomy of brown and red algae*: 206–217, figs 5, 6 (1978); Cabioch in *C. R. Hebd. Séanc.Acad. Sci., Paris,* D **288**: figs A–D, pl.1 (1979).

DESCRIPTION. Plants epiphytic, forming closely adherent discs or sleeves or partially free discs on hosts, to 6 mm diameter, 370 μm thick, margin usually thick but restricted bistratose areas occurring, mauvish (Methuen reddish lilac), somewhat chalky, surface smooth. Single layer of *axial filaments* with cells varying from tall, obliquely orientated, sinuate, often with a tapered base, to short, vertically orientated cells 7–98 μm high × 7–16 μm diameter, *erect filaments* to 20 cells long, cells 10–63 μm long × 5–20 μm diameter, not always horizontally aligned, *epithallial cells* domed, cell contents mainly sparse but lower cells sometimes with starch grains. *Gametangial plants* either monoecious or with spermatangial conceptacles only, *spermatangial conceptacles* (from two plants only) immersed, conceptacle chamber broadly triangular, 78–130 μm diameter, 39–52 μm high, spermatangia on conceptacle floor only; *carpogonial conceptacles* (from one population only) immersed, conceptacle chamber flask-shaped, 90–104 μm diameter, 39–59 μm high; *carposporangial conceptacle* (only one seen) slightly raised, conceptacle chamber rounded, 182 μm diameter, 130 μm high, roof 47 μm thick, small, thick, central fusion cell with peripheral gonimoblast filaments to five cells long; *tetrasporangial plants* not seen; *bisporangial conceptacles* completely immersed to somewhat raised, visible externally either as an ostiole only, or an ostiole surrounded by a pinkish roof with a white rim, 150–200 μm external diameter, conceptacle surface irregularly ridged, conceptacle chamber rounded to elliptical, 169–235 μm diameter, 75–117 μm high, roof 26–52 μm thick, roof



Figs 218–219 Vertical sections of *Titanoderma corallinae* conceptacles.
218. Bisporangial conceptacle (76/167) growing on *Melobesia membranacea* (M) on *Furcellaria*; the thallus cells are full of starch grains giving them a more dense appearance than is usual in this species.
219. Young carposporangial conceptacle (76/167).

composed of varying numbers of smallish cells, tapering to the ostiole, columella slightly- to well-developed, up to *c.* 20 *bisporangia*, 50–87 μm long × 39–59 μm diameter. Old conceptacles may become buried in the thallus.

HISTORICAL. *Melobesia corallinae* was described by the Crouan brothers (1867) as growing epiphytically on *Corallina officinalis*. It has remained as an unusually well-defined entity for a coralline species apart from being included in various genera or being regarded as a variety or form of the taxa now known as *T. pustulatum* var. *pustulatum* or var. *macrocarpum*. The present concept of *T. corallinae* is essentially the same as originally conceived by Crouan & Crouan (1867).

LECTOTYPE SPECIMEN (now designated). *Melobesia corallinae* P. & H. Crouan (1867: 150). France, Rade de Brest, Banc du Chateau et Baie de la Ninon, *P.-L. & H.-M. Crouan* (CO!) (Figs 208, 220, 221).

The only sample of *Melobesia corallinae* in evidence at Concarneau comprised two mounted *Corallina* plants (Fig. 208) bearing epiphytes. The plants bear both sleeve-like *Titanoderma* thalli and discoid, mushroom-like thalli measuring about 600 μm diameter. The latter are attached centrally and have free margins. The plants bear slightly raised tetra/bisporangial conceptacles measuring about 200 μm external diameter.

In VS the sleeve-like thallus (Fig. 221) is composed of rather short, vertically orientated axial cells which taper to the base, erect filaments are up to about seven cells long. The discoid thallus (Fig. 220) has tall, obliquely orientated axial cells and erect filaments up to three cells long, the free margins appearing to have regenerated from cells of the erect filaments. Cells of axial filaments measure 10–50 μm high × 3–7 μm diameter and those of erect filaments are 9–45 μm long × 5–10 μm diameter. Epithallial cells are triangular to domed. Conceptacle chambers are elliptical to rounded, measuring *c.*180 μm diameter and 110 μm high; the roof measures 27–45 μm thick. The plants are probably bisporangial but the long-dried sporangia are difficult to identify with certainty.

The host *Corallina* plants appear stunted, as is characteristic when *T. corallinae* is present (Cabioch, 1979).

PLANT APPEARANCE. The most characteristic appearance of *T. corallinae* is as a small, rather thick, pale mauvish (Methuen reddish lilac) epiphyte, with a smooth surface, that grows on *Corallina officinalis* (Figs 209, 212), where it varies from applanate discoid, to being centrally attached with detached, lobed edges, to entirely encircling the host thallus. It also grows on non-calcified red algae, in particular *Furcellaria lumbricalis*.

The mature thallus surface (Figs 211, 213) resembles marginal areas of young thallus (Fig. 216) in appearing to comprise radiating filaments of elongated cells with epithallial concavities. However, as the mature surface is composed of cells of vertically orientated erect filaments, the radiating appearance must have a different origin from the thallus margin which comprises axial filaments. This appearance is characteristic of *T. corallinae,* and to some extent *T. laminariae*, and is distinctively different from the honeycomb-like surface of most mature *Titanoderma* thalli. Bisporangial conceptacles are immersed or slightly raised (Figs 212, 213), appearing more raised in dried material than fresh. Their roof surface is composed of haphazardly arranged, irregularly calcified cells (Fig. 215).

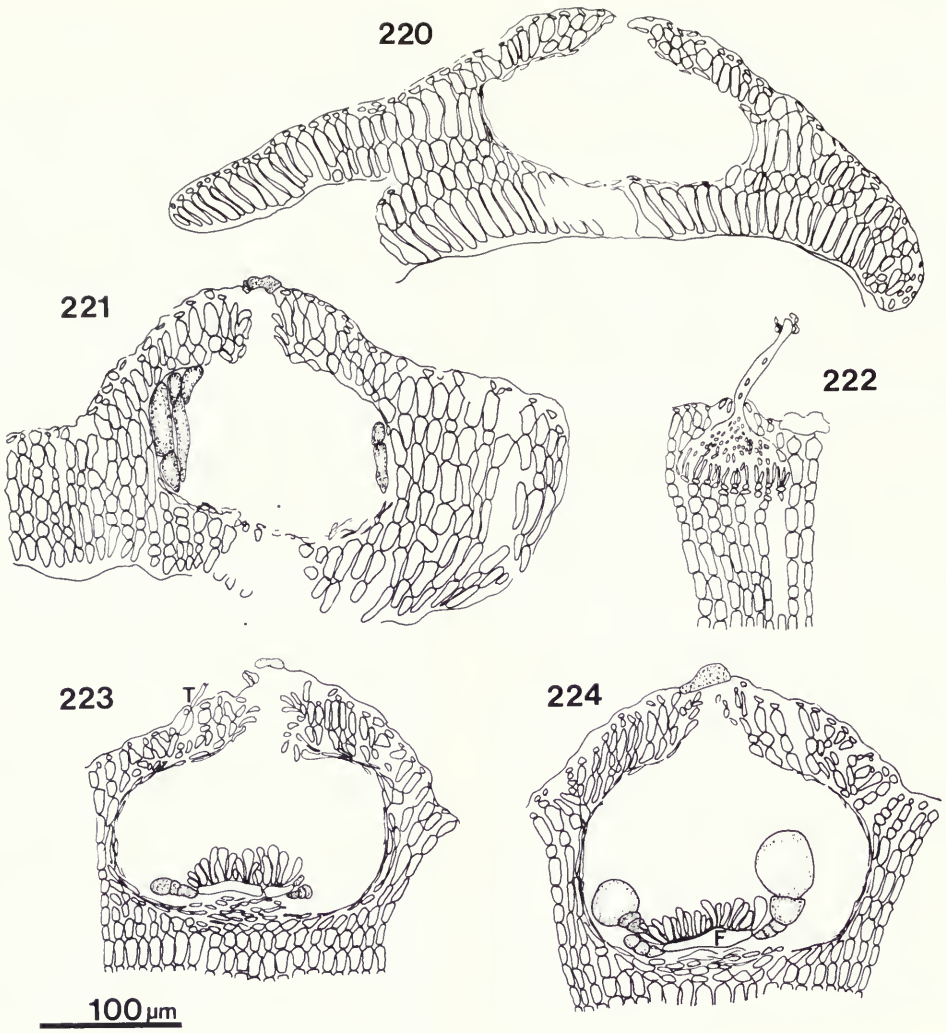
VEGETATIVE ANATOMY. The thallus of *T. corallinae* is composed of erect filaments, contiguous cells of which may or may not be aligned horizontally (Figs 52j, 214, 218, 219). The cells often appear to be nearly empty, although plants with their lower cells full of starch grains also occur (Fig. 218). Axial cells tend to taper towards the base (Fig. 52j) and although this may be partly due to the direction of sectioning, it occurs more frequently in this species than others. Tapering has been mentioned as a characteristic feature by various authors (e.g. Masaki & Tokida, 1960*a*) and is evident in drawings by Suneson (1943, fig. 24). The predominant lack of a thin thallus margin has been used as an identifying characteristic of this species (Rosenvinge, 1917; Suneson, 1943, figs 24B; Hamel & Lemoine, 1953) and British Isles material confirms this character. The rather narrow cells, thick thallus, and flat conceptacles of *T. corallinae* resemble *T. laminariae* but the much smaller tetra/bisporangial conceptacle size (Figs 52j–k) of *T. corallinae* is sufficient to distinguish between the species.

GAMETANGIAL PLANTS. Only two samples of gametangial plants have been found during this study. Although it is probably impossible to recognize different conceptacle types externally, a large number of plants with apparently differing conceptacle sizes were sectioned and nearly all proved to have bisporangial conceptacles in varying stages of development. Suneson (1943, in Sweden) and Masaki & Tokida (1960*a*, in Japan) both found gametangial plants apparently quite commonly and, although they do not give dates of collection, it is possible that such plants occur mainly in summer whereas most of my collections were made during winter. One of the plants, collected at Fife Ness on the east coast of Scotland in August 1976 (76/167) is dioecious, the other plant (Bembridge, January 1979, 79/17) is spermatangial only. This agrees with Suneson (1943: 45) who found mainly dioecious plants but some with only spermatangia, and Masaki & Tokida (1960*a*: 285) who report spermatangial conceptacles as 'sometimes co-existing with female conceptacles'. In *Fosliella farinosa,* Chamberlain (1977) found that gametangial plants were dioecious in summer but spermatangial plants occurred in winter.

SPERMATANGIAL PLANTS. Small, flask-shaped spermatangial conceptacles (Fig. 222) occur near the thallus surface and become immersed in the thallus as they age. Ostioles may be prolonged into a spout (Fig. 222) which may widen (Fig. 16) as the conceptacle becomes immersed (Suneson, 1943). Spermatangial initials cut off elongate spermatangia that round off on release (Fig. 222) and conceptacles often contain spermatangia even when completely immersed.

The conceptacles agree closely with Suneson's (1943) material, but Japanese conceptacle chambers (Masaki & Tokida, 1960*a*) are somewhat larger measuring 95–140 μm diameter × 55–85 μm high.

CARPOGONIAL/CARPOSPORANGIAL PLANTS. Carpogonial conceptacles originate in subepithallial initials as shown by Masaki & Tokida (1960*a*, pl.V, fig. 1). Both Masaki & Tokida and Suneson (1943) (see Fig. 17) show that fertile cells develop across the floor of the conceptacle, bearing one or two carpogonial branches centrally and sterile cells peripherally. Carpogonial conceptacle chambers measure 90–104 μm diameter × 39–59 μm high in the British Isles compared with about 72 μm × 45 μm in Suneson's drawing and 110 μm × 50–85 μm recorded by Masaki & Tokida (1960*a*). After presumed fertilization, a fusion cell develops



Figs 220–224 Vertical sections of gametangial conceptacles of *Titanoderma corallinae* growing on *Corallina*.

220 & 221. Conceptacles (probably bisporangial) of the lectotype specimen of *Melobesia corallinae* (CO). Fig. 220 is a discoid thallus with free margins; Fig. 221 is a sleeve-like thallus, note the tapering axial cells.

222. Spermatangial conceptacle (76/167). Elongate attached spermatangia round off on release.

223. Young carposporangial conceptacle (76/167) showing the initiation of gonimoblast filaments (shaded) from the periphery and underside of the fusion cell; carpogonial remnants on the surface of the fusion cell have become swollen and somewhat clavate. A trichocyte (t) occurs in the roof.

224. Mature carposporangial conceptacle (76/167), F=fusion cell.

on the conceptacle floor (Fig. 223) and gonimoblast filaments (Fig. 224) are initiated at the periphery. A trichocyte is seen in the roof (Fig. 223). The only mature carposporangial conceptacle found (Figs 219, 224) measures 182 µm internal diameter × 130 µm high with the roof 47 µm thick, which compares with 166 µm × 77 µm in Suneson's drawing (1943) (see Fig. 18) and 165–210 µm × 105–155 µm recorded for Japan (Masaki & Tokida, 1960*a*). Gonimoblast filaments (Fig. 224) are five cells long including the terminal carposporangium and carpogonial remnants on the surface of the fusion cell become clavate (Fig. 224). The conceptacle roof is about three to four cells deep, the cells are irregularly sized and trichocytes occur. The fusion cell and gonimoblast filament (Figs 219, 224) are noticeably small in relation to the conceptacle chamber.

Suneson (1950) made a cytological study of carpogonia in this species and established a haploid chromosome count of n = 16.

BISPORANGIAL PLANTS. The bisporangial phase is predominant in the British Isles, Denmark (Rosenvinge, 1917), Sweden (Suneson, 1943), and Pacific Mexico (Dawson, 1960), but only tetrasporangia are found in Japan (Masaki & Tokida, 1960*a*). Mature conceptacle chambers are similar in size to those recorded by Suneson (1943) and to those of tetrasporangial conceptacles in Japan (Masaki & Tokida, 1960*a*). The conceptacle roof (Figs 52j, 218) is similar in structure to that of the carposporangial conceptacles and there is usually a well-defined central columella. Up to about 20 bisporangia are borne peripherally on stalk cells, they are similar in size to those recorded by Suneson (1943).

Only bisporangia with uninucleate bispores have been found in the British Isles but Suneson (1950) found occasional tetrasporangia and quadrinucleate bisporangia (with binucleate bispores) mingled with binucleate bisporangia in Sweden. Cytological studies (Suneson, 1950) showed that uninucleate

bispores were diploid and were derived mitotically from a diploid plant, whereas meiosis occurred in the production of tetraspores and binucleate bispores from diploid plants. Suneson (1950: 448) deduced that a normal *Polysiphonia*-type life history involving gametangial/carposporangial and tetrasporangial (or quadrinucleate bisporangial) plants occurred, together with a separate, apomictic cycle with diploid plants and bispores. He further suggested that 'the pronounced polymorphy in northern populations of the encrusting Corallinaceae seems to be connected with the apomeiotic bispore formation'.

SPORE GERMINATION. The pattern of spore germination in *T. corallinae* (as *Dermatolithon)* was studied by Chihara (1974*a*) who classified it as belonging, like other Lithophylloideae, to the *Amphiroa*-type pattern. Notoya (1974) investigated three species of *Titanoderma* (as *Tenarea corallinae, T. tumidulum*, and *T. canescens*) and deduced a general pattern of *Titanoderma* germination on this basis (Fig. 1). A scanning electron micrograph of a young sporeling (Fig. 3) shows eight principal epithallial concavities on the surface with the two central pairs being closely adjacent, conforming with the pattern seen under optical microscopy in *T. pustulatum* (Figs 2, 4). Two distinct patterns of growth appear to occur in *T. corallinae* sporelings on *Corallina* intergenicula. In one (Fig. 216) a discoid crust develops which has the remains of the original sporeling perched on the surface, while in the other a branched thallus develops (Fig. 217). Possibly this occurs when two bispores of a bisporangium develop adjacent to one another. Eventually both types of growth create similar adult plants.

When *T. corallinae* spores germinate on the adaxial side of a *Corallina* intergeniculum (Fig. 210) the surface of the intergeniculum surrounding the sporeling becomes colourless. Cabioch (1979) made a detailed study of this phenomenon, which she regards as semi-parasitism, and showed that the epiphyte destroys the epithallial cells and initials of the host which responds by regenerating thallus cells, but these in their turn are destroyed. Cabioch assumes that chemical interactions form a crucial role in this destructive epiphytism but studies to confirm this have not been made, nor is it established whether the epiphyte derives any nutritional benefit from the host.

Cabioch (1979) shows that semi-parasitism is not obligatory in *T. corallinae* because spores will germinate normally on a glass slide. However, she is not convinced that, as reported by Suneson (1943), the species grows on red algae other than *Corallina*. In my study I have found *T. corallinae* on a number of, mainly red, algal hosts, but most frequently on *Furcellaria lumbricalis*. Very often it does not grow directly on the host but on an intervening thallus of *Melobesia membranacea*. Possibly the presence of another calcareous alga aids germination as usually seems to be the case with *Mesophyllum lichenoides* (Ellis) Lemoine, which is another epiphyte on *Corallina*. As Cabioch (1979) shows, the destructive effect of *T. corallinae* is permanent because old intergenicula which have shed the epiphyte retain a damaged and irregular surface, a feature seen frequently on British Isles *Corallina* plants (Fig. 209).

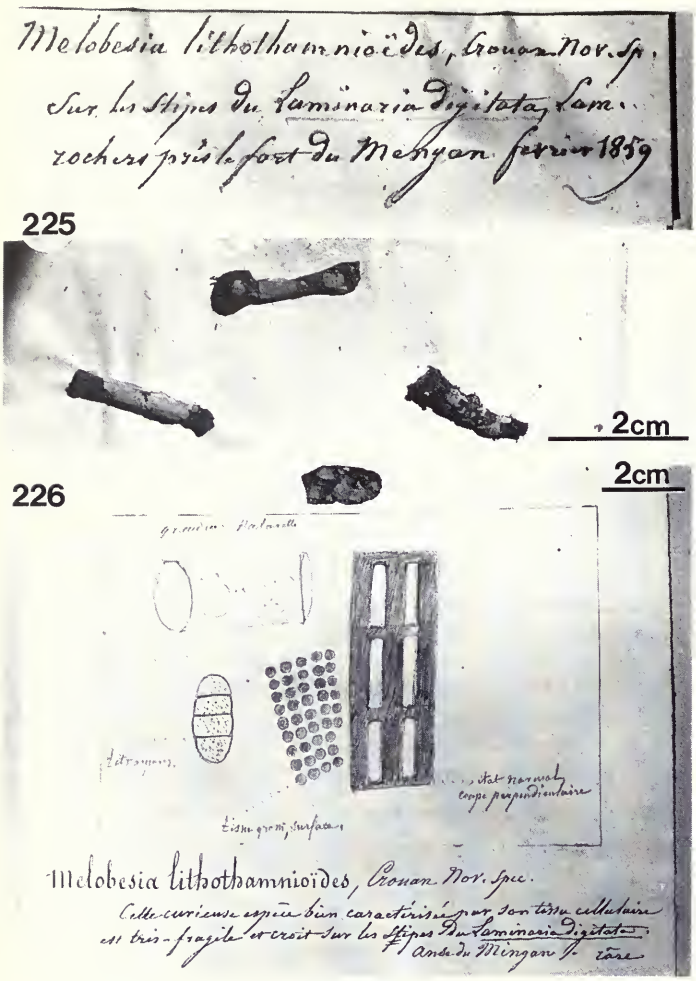
DISTRIBUTION. *British Isles*: From all parts of the British Isles where suitable plant hosts occur, that is to say virtually throughout except for parts of the east coast south of Yorkshire. *World*: Baltic, Sweden, Denmark, Faeroes, northern and western France, Spain, Mediterranean, Canary Islands, South Africa, Japan, southern USSR, Atlantic and Pacific coasts of North America, southern Australia, New Zealand. [Probably cosmopolitan].

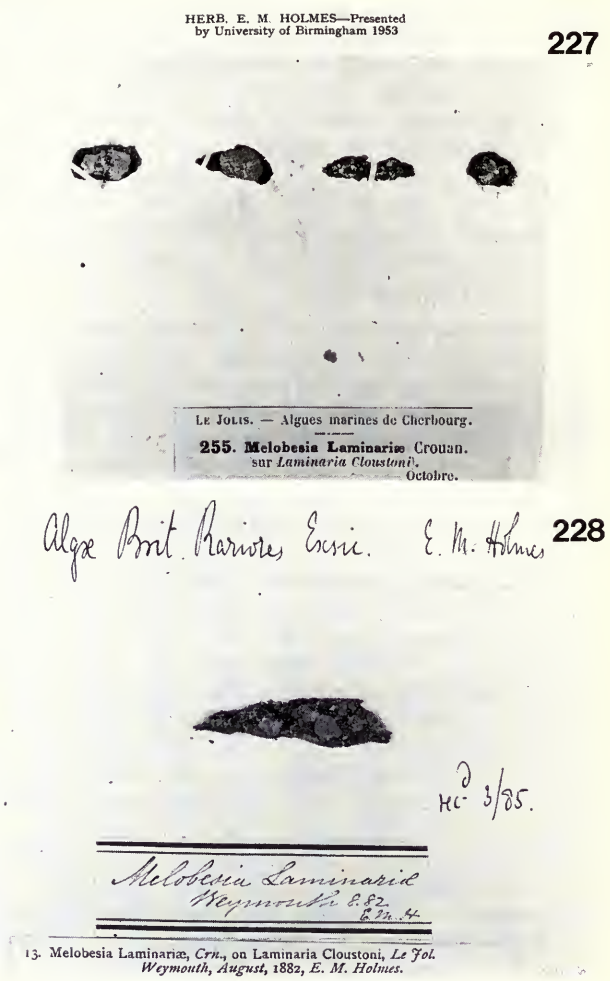
HABITAT AND PHENOLOGY. *Titanoderma corallinae* grows mainly on *Corallina officinalis* and is common in rock pools from mid tide level downwards throughout the British Isles; Suneson (1943, 1950), however, records it as occurring only in the lower subtidal in western Sweden. It also grows on the following hosts: *Laminaria digitata*, *Cystoseira baccata* (Gmelin) Silva, *Pterocladia capillacea*, *Furcellaria lumbricalis, Chondrus crispus, Palmaria palmata, Laurencia pinnatifida*, and *Polysiphonia nigrescens*. An association of algae (see p. 58) growing in shallow pools on low tide level ledges at Bembridge was observed sequentially from 1975 to 1977; *T. corallinae* grew on *Corallina* and *Furcellaria*, in company with *T. pustulatum* var. *confine* (including the minute growth form). On *Furcellaria* it often grew on either *Melobesia membranacea* or var. *confine* rather than the actual host alga (Fig. 170).

Titanoderma corallinae occurs and produces conceptacles throughout the year but it is not known whether the conceptacles are always fertile. It is suggested (p. 67) that gametangial plants may occur in summer rather than winter, but the evidence for this is mainly negative. Goss-Custard et al. (1979: 18) studied the percentage cover of *T. corallinae* (as *Dermatolithon*) on *Corallina* growing in intertidal pools at Lough Ine, southern Ireland. They found fluctuating quantities without a pronounced seasonal correlation.

HERBARIUM SPECIMENS CONFIRMED AS T. CORALLINAE. As *Melobesia corallinae* and *M. hapalidioides* f. *confinis*, British Isles, Devon, Torquay, on *Corallina*, March 1883, *E. M. Holmes* (BM!) *(T. pustulatum* var. *confine* also present); as *Melobesia corallinae*, British Isles, Cornwall, The Lizard, on *Corallina*, July 1882, *E. M. Holmes*, Alg.Br.rar. Exsicc., Fasc.I, no. 12 (BM!); British Isles, Ayr, Cumbrae, on *Corallina*, August 1891, *E. A.Batters* (BM!); British Isles, Northumberland, Berwick, on *Corallina*, January 1887, *E. A.Batters* (BM!); as *Melobesia corallinae* and *M?. verrucatum* (also as an indet. specimen), British Isles, Northumberland, Berwick, on *Corallina* and *Gelidium pusillum*, October 1884, *E. A. Batters* (BM!) (var. *confine* also present). British Isles specimens in herb. *Chamberlain*: Fife, Fife Ness, on *Corallina*, intertidal, 16 August 1976, 76/167; Glamorgan, Port Eynon, on *Corallina*, intertidal, 19 August 1978, 78/190; Hampshire, Isle of Wight, Bembridge, in the Run, on *Corallina*, intertidal, 13 November 1978, 78/305; Hampshire, Isle of Wight, Bembridge, the ledges, on *Furcellaria lumbricalis* with *T. pustulatum* var. *confine*, intertidal, 27 June 1979, 79/208; Co.Clare, Newquay Rapids, on *Furcellaria,* intertidal, 2 December 1982, 82/99; Devon, Wembury, on *Corallina*, intertidal, 24 November 1988, 88/124.

3. **Titanoderma laminariae** (P. & H. Crouan) Y. Chamberlain, **comb.nov.**— *Melobesia laminariae* P. & H. Crouan, *Fl. Finistère*: 150 (1867).—*Dermatolithon laminariae* (P. & H. Crouan) Foslie in *K.nor. Vidensk.Selsk.Skr.* **1899**(7): 13 (1900) pro parte (as to Le Jolis, Alg.mar.Cherbourg: 255)—*Lithophyllum macrocarpum* f. *laminariae* (P. & H. Crouan) Foslie in *K.nor. Vidensk.Selsk.Skr.* **1900**(5): 22 (1900).—*Lithophyllum pustulatum* f. *laminariae* (P. & H. Crouan) Foslie in *K.nor.Vidensk.Selsk.Skr.* **1905**(3): 118, 128 (1905) pro parte. Type: under herbarium name

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227
Le Jolis. — Algues marines de Cherbourg.
255. Melobesia Laminariæ Crouan.
sur Laminaria Cloustoni.
Octobre.
Algæ Brit. Rariores Exsic. E. M. Holmes
228
Melobesia Laminariæ
Weymouth E.82
13. Melobesia Laminariæ, Crn., on Laminaria Cloustoni, Le Jol.
Weymouth, August, 1882, E. M. Holmes.

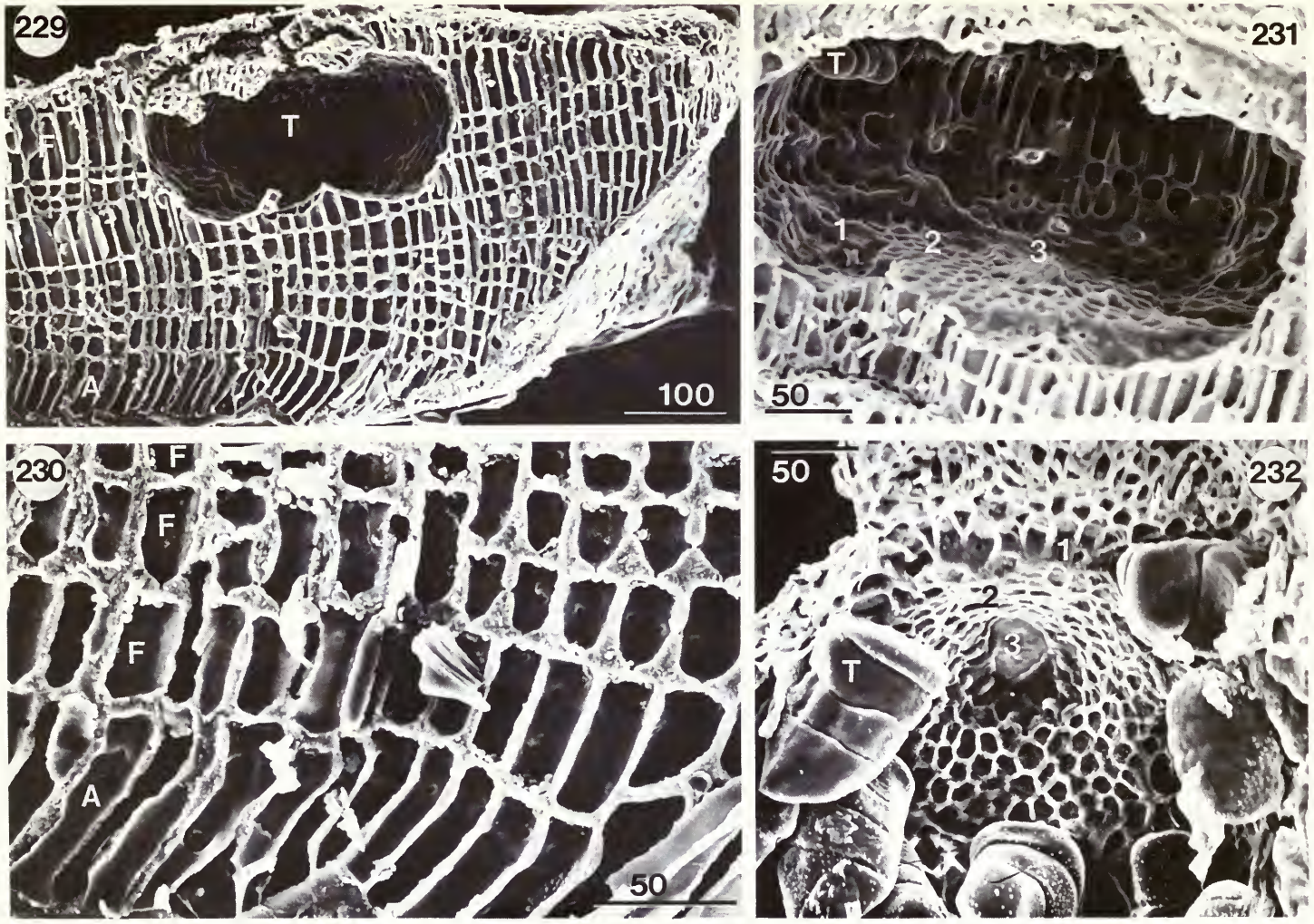
Figs 225–228 Historical specimens of *Titanoderma laminariae*.
225. Lectotype specimen of *Melobesia laminariae*. (CO). The label on the outside of the packet is above and the specimens inside the packet are below.
226. Isolectotype specimen of *Melobesia laminariae* (CO).
227. Le Jolis's specimen (no.255) of *Melobesia laminariae* (BM).
228. E. M. Holmes's specimen of *Melobesia laminariae* (BM)

Melobesia lithothamnioides, France, Cherbourg, rochers pres le fort du Mengan, sur les stipes du *Laminaria digitata* Lam., *P.-L. & H.-M. Crouan* (CO!—lectotype selected here (Fig. 225); CO!—isolectotype).
Figs 52k, 225–247.

ILLUSTRATION. As *Dermatolithon crouanii* in Hamel & Lemoine, *Archs Mus. natn.Hist.nat.Paris* VII, **1**: 62, fig. 24 (1953).

DESCRIPTION. Plants epiphytic, adherent, fragile, flat, to 20 mm diameter, 500 μm thick, mauvish, somewhat chalky, surface smooth.

Single layer of *axial filaments* with cells usually tall and often sinuate, cells 13–52 μm high × 6–13 μm long, *erect filaments* to 20 cells long, cells 6–39 μm long × 7–15 μm diameter, not always horizontally aligned, *epithallial cells* flattened to domed, cytoplasmic cell contents sparse, small starch grains (to 3.5 μm diameter) frequent in lower thallus cells. *Gametangial plants* mainly dioecious, occasionally monoecious, *spermatangial conceptacles* immersed, roof slightly raised, conceptacle chamber broadly triangular, 97–127 μm diameter, 22–33 μm high, roof 10–20 μm thick, with or without a spout, spermatangia on conceptacle floor only, conceptacles becoming buried in layers in thallus; *carpogonial conceptacles* immersed, conceptacle chamber flask-shaped, 130–169 μm diameter, 52–78 μm high; *carposporangial conceptacles* immersed, roof slightly sunken to slightly raised, to 300 μm external diameter, conceptacle chamber elliptical, broad ostiole canal tapering to thallus surface and surrounded by papillae, 208–290 μm diameter, 52–117 μm high, roof 39–52 μm thick and near ostiole mainly composed of epithallial and two elongated cells, fusion cell wide and thin with gonimoblast filaments to five cells long emanating from lower surface at periphery; *tetrasporangial conceptacles* immersed, roof slightly sunken to slightly raised, to 300 μm external diameter, roof surface honeycomb-like, conceptacle chamber elliptical, ostiole canal tapering somewhat to thallus surface but not surrounded by conspicuous papillae, chamber 312–364 μm diameter, 104–156 μm high, roof 42–94 μm thick and near ostiole composed of epithallial and two elongated cells,

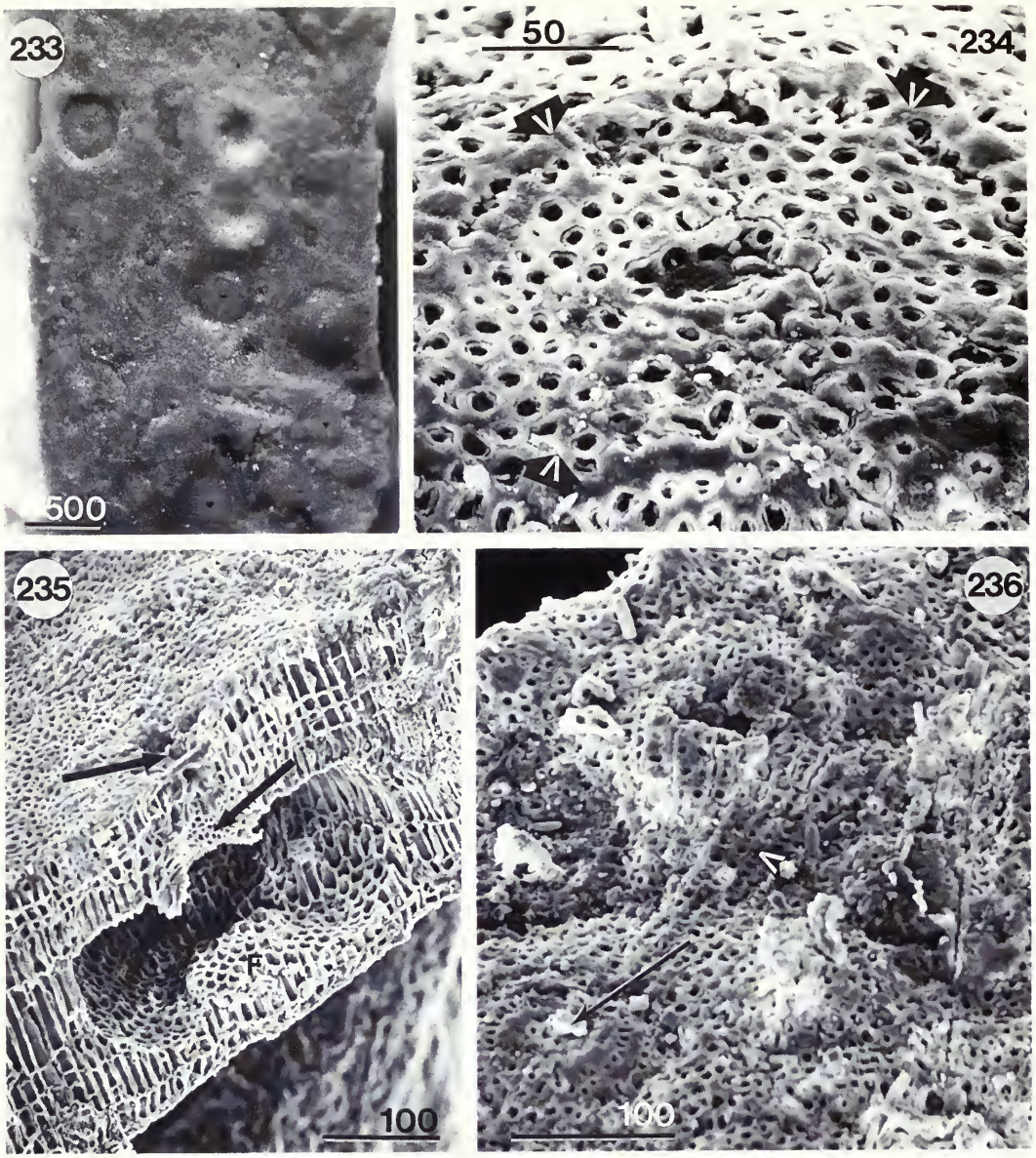


Figs 229–232 Scanning electron micrographs of tetrasporangial plants of *Titanoderma laminariae* (scales in μm).

229. Vertical fracture of *Le Jolis* 255 showing tetrasporangial conceptacle (T) near the characteristically thick thallus margin. Contiguous cells of erect filaments (F) are not horizontally aligned, axial cells (A) are more or less oblique.

230. Detail of erect filament (F) and axial (A) cells from Fig. 229.

231 & 232. Vertical fracture (Fig. 231) and view from above (Fig. 232) of tetrasporangial conceptacles showing the peripheral ring (1) where tetrasporangia (T) have been attached, the basal remants (2) of the conceptacle chamber cells, and the columella (3) (cf. Fig. 247); Fig. 231 is from *Le Jolis* 255; Fig. 232 is from 83/225.



Figs 233–236 Gametangial plants of *Titanoderma laminariae* (scales in μm).

233. Carposporangial conceptacles varying from slightly sunken to slightly raised (86/134).

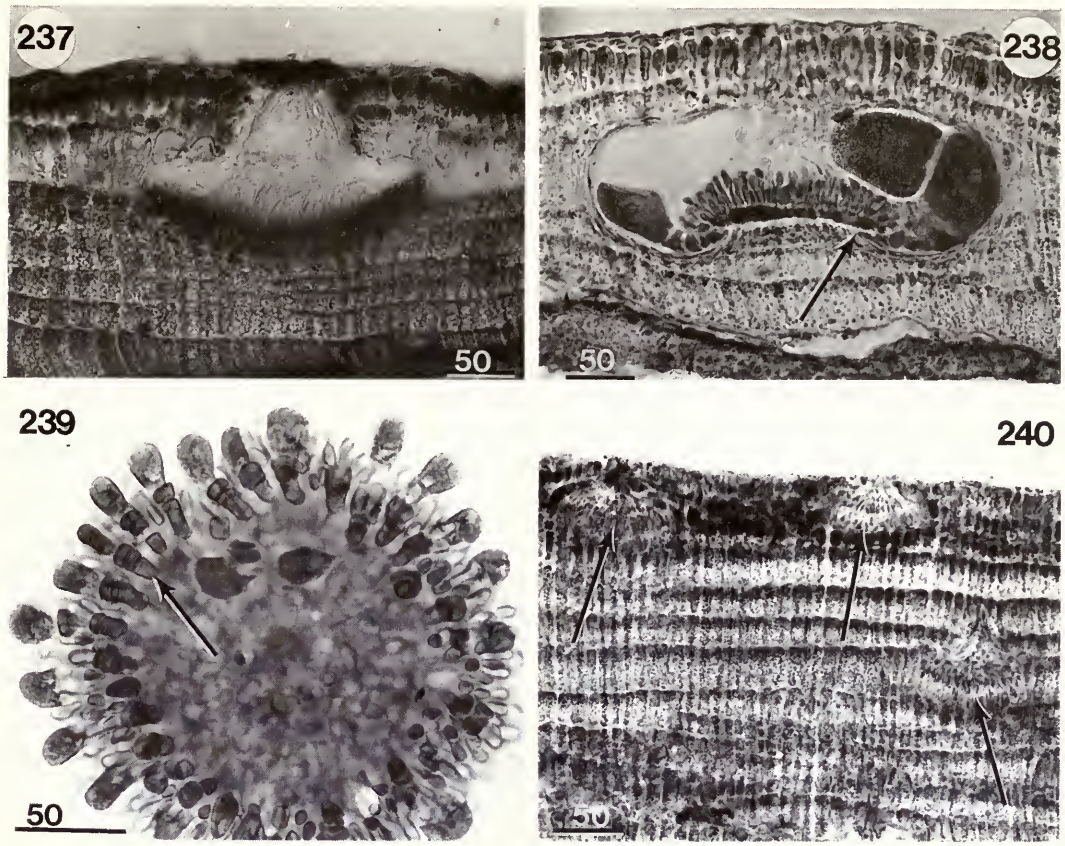
234. Roof of slightly sunken caposporangial conceptacle. Arrows mark the conceptacle periphery (83/225).

235. Vertical fracture of carposporangial conceptacle, the ostiole can be seen from the surface and from below (arrows), and the point of attachment (F) of the fusion cell can also be seen (86/134).

236. Surface view of spermantangial plant. The conceptacle spout (arrow) can be seen in the centre of the domed conceptacle roof, as can the irregular nature of the thallus surface and frequently filamentous appearance (e.g. arrow head) of the cells (83/225).

columella usually well-developed, *tetrasporangia* 75–112 μm long × 39–68 μm diameter; *bisporangial conceptacles* not seen. Old tetrasporangial conceptacles may become buried in the thallus.

HISTORICAL. The Crouan brothers (1867) described *T. laminariae* as a violet brown 'fronde' growing on the stipes of *Laminaria digitata*, and this description agrees well with the plants (Figs 225, 226) in their herbarium at Concarneau to which they gave the herbarium name *Melobesia lithothamnioides*. Foslie (1898*c*: 17) had not seen this material when he first discussed the probable identity of the species, although he correctly identified it with *Melobesia laminariae*, Le Jolis, Alg.mar.Cherbourg 255. In the same publication Foslie concluded that further material, which was similar in appearance and often grew with *T. laminariae*, was really a distinct species which he named *Lithophyllum crouani(i)*. He designated as type a specimen collected by Batters at Berwick-upon-Tweed, which is a true *Lithophyllum* and is the entity which has incorrectly become known as *L. orbiculatum* (Foslie) Foslie (e.g. Adey & Adey, 1973) (see Chamberlain et al., 1988). Norwegian specimens from Frøjen (11 July 1894) (PC!) and Kristiansund (9 August 1898) (BM!, TRH!), collected by Foslie and identified as *L. crouanii,* are both true *L. crouanii.* Material from Kristiansund identified by Foslie



Figs 237–240 Gametangial plants of *Titanoderma laminariae* (scales in μm).

237. Vertical section of carpogonial conceptacle (86/134/5) with a concave conceptacle floor.

238. Vertical section of nearly mature carposporangial conceptacle (86/134/5). Gonimoblast filaments arise from the lower surface of the fusion cell (arrow); the upper surface of the fusion cell bears clavate cells that have developed from old carpogonial branches.

239. Under surface of detached fusion cell (86/134/5) showing young gonimoblast filaments (arrow) arising from the lower surface.

240. Vertical section of spermatangial conceptacles (arrows) that become immersed in the thallus but still contain spermatangia (83/490).

as *Choreonema laminariae* (BM!) is *Titanoderma pustulatum* var. *pustulatum* which commonly grows on *Laminaria* holdfasts in Britain and France.

These three quite distinct entities were included by Foslie within *laminariae* and *crouanii* (Table 3) and it is the widespread *pustulatum* entity which has come to be known most usually as *Dermatolithon pustulatum* f. *laminariae* (e.g. Newton, 1931: 306, as *Lithophyllum*; Hamel & Lemoine, 1953: 60), while the less common *T. laminariae* has been referred to as *Dermatolithon crouanii* (Hamel & Lemoine, 1953: 62). Foslie's publications (1898*c*, 1900*b*, 1905*a*) are very confusing concerning the identity of, and specimens pertaining to, the three species involved (Table 3); however, three Le Jolis specimens, number 255 of Alg mar. Cherbourg (Figs 227, 229–231), and numbers 2332 and 2354 (CHE!, BM!), all of which are widely distributed, are good examples of *T. laminariae*.

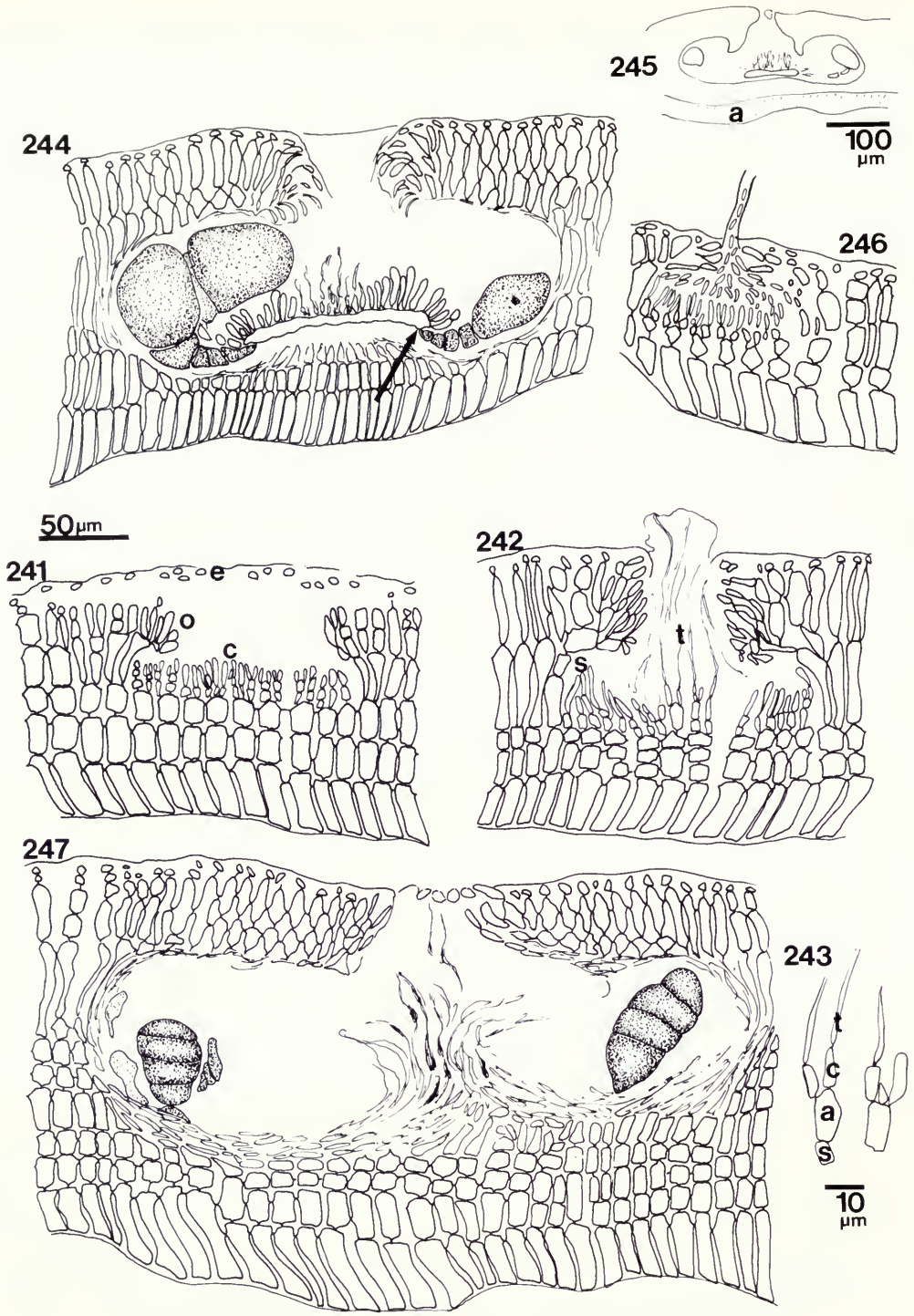
Mazza (1917: 201) refers to the Le Jolis, Alg.mar.Cherbourg 255 record and remarks that Chalon was of the opinion that these plants were young thalli of *Phymatolithon lenormandii*.

NOTES ON TYPE AND OTHER HISTORICAL SPECIMENS. (1). *Melobesia laminariae* P. & H. Crouan (1867: 150). Lectotype (now designated): France, Cherbourg, rochers pres le fort du Mengan, sur les stipes du *Laminaria digitata*, février 1859, *P.-L. & H.-M. Crouan* (CO!) (Fig.225). Also isolectotype (CO!) (Fig.226).

Two samples (Figs 225, 226) of *Titanoderma laminariae* are present in Concarneau, both under the Crouans' herbarium name of *Melobesia lithothamnioides*. The sample without drawings (Fig. 225) has been chosen as lectotype. It comprises three pieces of *Laminaria* stipe bearing fragments of brittle, dull mauvish thallus with small, flat conceptacles visible on the surface; *Melobesia membranacea* is also present. A section of the thallus shows somewhat oblique axial filament cells measuring 23–54 μm high × 10–16 μm diameter. Erect filaments are up to four cells long with cells measuring 9–64 μm long × 9–14 μm diameter, contiguous cells are not aligned. Further examination was not carried out because the thalli are scarce and brittle, but the Crouans' drawing (Fig. 226) shows that tetrasporangial conceptacles are present on the sample that can be regarded as an isolectotype.

(2). *Melobesia laminariae* P. & H. Crouan: France, Cherbourg, sur *Laminaria cloustoni*, Octobre, *Le Jolis*, Alg. mar. Cherbourg 255 (BM!) (Figs 227, 229–231).

Le Jolis's material (Fig. 227) is widely distributed as an exsiccata and forms a useful exemplar for *T. laminariae*. The plant from the exsiccata in BM shows the characteristically non-aligned thallus cells (Fig. 229, 230), oblique axial cells (Fig. 230), and a tetrasporangial conceptacle (Fig. 231). The thallus



Figs 241–247 Vertical sections of reproductive features of *Titanoderma laminariae*.

241. Young carpogonial conceptacle (78/80) with immature carpogonial branches (c). The old epithallial cells (e) are being shed from the thallus surface and ostiole filaments (o) are beginning to form. The 50 µm scale applies to all figures except Figs 243 and 245.

242. Older carpogonial conceptacle (78/80) with fertile branches carrying trichogynes (t) in the centre and sterile branches (s) peripherally; development of ostiole filaments continues.

243. Two fertile branches comprising a supporting cell (s), auxiliary cell (a), carpogonium (c), and trichogyne (t); a small sterile cell is present on the right hand branch.

244. Mature carposporangial conceptacle (86/134/3) with gonimoblast filaments arising from the under surface (arrows) of the fusion cell and clavate cells on the surface of the fusion cell.

245. Diagrammatic drawing to show the characteristic shape of a mature carposporangial conceptacle (86/134/14). a = axial filaments.

246. Spermatangial conceptacle (86/134/14) with elongated attached spermatangia and ovate released spermatangia moving into the spout.

247. Tetrasporangial conceptacle (85/191) with peripheral tetrasporangia and a prominent, central columella.

surface appears heavily calcified and the epithallial cavities are somewhat inconspicuous.

PLANT APPEARANCE. *Titanoderma laminariae* grows on the holdfasts and stipes of *Laminaria hyperborea* and *L. digitata,* forming brittle, but rather thick, smooth crusts which usually have a thick margin. Herbarium plants from France (e.g. *Le Jolis* 255, cited above) are usually a deep mauve colour, as described by the Crouans (1867). Many of the English plants collected during this investigation are drift material and bleached, but a population of carpogonial/carposporangial plants (86/134) is somewhat redder (Methuen—dark ruby) and has bistratose margins. Hamel & Lemoine (1953) on the other hand, described living plants (as *Dermatolithon crouanii*) as being pale, shiny purple, and live material that I collected in France was purplish when fresh.

The thallus surface in marginal areas is composed of radiating filaments of elongated cells with large epithallial concavites. To some extent this structure continues in central areas (Fig. 236), as in *T. corallinae*. The surface may otherwise become honeycomb-like as it ages. Tetrasporangial (Fig. 234) and carposporangial (Fig. 233) conceptacle roofs are disc-like and vary from slightly sunken to slightly raised, spermatangial roofs are domed (Fig. 236), and usually have central spouts. Immersed conceptacles are usually sufficient to distinguish the species from *T. pustulatum* var. *pustulatum* with which *T. laminariae* is often closely associated. It is more difficult, however, to distinguish it externally from *Lithophyllum crouanii* and the species have frequently been confused (Table 3).

VEGETATIVE ANATOMY. In VS (Figs 52k, 229, 230, 247) the thallus is composed of elongate, oblique, sometimes sinuate axial cells and erect filaments up to 20 cells long with vertically elongated cells that vary considerably in length and are not always in aligned rows. Cytoplasmic contents tend to be sparse and chiefly located at the tops of cells. Starch grains up to 3.5 μm diameter occur commonly in the lower thallus cells. The thallus margin is usually thick (Fig. 229), but attenuated, bistratose margins occur in plants that have probably grown particularly fast.

SPERMATANGIAL PLANTS. Spermatangial conceptacles occur at the thallus surface (Figs 236, 240, 246) and have relatively wide shallow chambers. Elongated spermatangia are borne on initials on the conceptacle base (Fig. 246); they round off and are released through a spout. Old conceptacles are buried in the thallus and may occur many layers deep (Fig. 240).

CARPOGONIAL/CARPOSPORANGIAL PLANTS. Carpogonial conceptacle primordia arise as discs in the subepithallial initials, later becoming immersed by growth of surrounding filaments (Fig. 241). Mature conceptacles (Figs 237, 242) have a concave floor from which fertile carpogonial branches (Fig. 243) arise centrally and sterile ones peripherally. The fertile disc is surrounded by stretched cells with swollen tops; when mature a deep ostiole canal develops through which the trichogynes protrude.

Mature carposporangial conceptacles (Figs 235, 238, 244) have a relatively broad, shallow chamber with a characteristic shape (Figs 235, 245) imparted by a broad ostiole canal which tapers upwards and is surrounded below by small, downward-pointing papillae. The roof is composed of an epithallial cell and one or two elongate cells (Fig. 244). A broad, shallow fusion cell (Figs 235, 238, 244) develops on the chamber floor; on its upper surface old carpogonia occur centrally and clavate sterile cells peripherally. The fusion cell appears to be attached to the conceptacle floor only at its centre (Figs 235, 238, 244) and gonimoblast filaments up to five cells long develop from the underside of its periphery (Figs 238, 239, 244).

Although mainly dioecious, a single thallus was observed that bore spermatangial and carposporangial conceptacles side by side.

TETRASPORANGIAL PLANTS. Like carposporangial conceptacles, mature tetrasporangial conceptacles have relatively broad, shallow chambers (Figs 52k, 229, 247). The roof is three cells thick including the epithallial cell (Fig. 247), and the ostiole canal tapers upward but is less elaborate than the carposporangial one. A conspicuous columella develops in the centre of the chamber (Fig. 247) and tetrasporangia are borne peripherally on stalk cells.

DISTRIBUTION. *British Isles*: Shetland Isles, Dorset, Devon (north and south coast). *World*: Northern France.
[*Titanoderma laminariae* is a subtidal plant and is not particularly conspicuous. It is probable that it will prove to be more widely distributed than is confirmed at present.]

HABITAT AND PHENOLOGY. The species is known predominantly as an epiphyte on *Laminaria* stipes and, particularly, holdfasts but has also been found on *Palmaria palmata* and *Laurencia pinnatifida*. It is only known to occur in low intertidal pools and subtidally and is presumably unable to tolerate desiccation. From the scanty material available at present, French plants would appear to be thicker, smoother, and generally more robust and conspicuous than English ones. This species usually occurs together with other epiphytic corallines, in particular *T. pustulatum* var. *pustulatum, Lithophyllum crouanii*, and *Melobesia membranacea*. Fertile material was collected throughout the year and spermatangial, carposporangial, and tetrasporangial plants were found in about equal numbers.

HERBARIUM SPECIMENS CONFIRMED AS T. LAMINARIAE. As *Melobesia laminariae*, France, Cherbourg, *Le Jolis,* Alg.mar. Cherbourg 255 (CHE!, BM!) (Figs 227, 229–231); France, Cherbourg, *Le Jolis* nos 2332, 2354 (BM!); France, Cherbourg, on *Laminaria*, 27 December 1876, Herb.Thuret, *E. Bornet* (BM-K!) [*Lithophyllum crouanii* also present]; British Isles, Dorset, Weymouth, on *Laminaria cloustoni*, August 1882, *E. M. Holmes*, Alg.Brit.Rar.Exsicc. Fasc.I, no. 13 (BM-K!) (Fig. 228); British Isles specimens in herb. *Chamberlain*: Cornwall, Rosemullion, on *Palmaria palmata*, intertidal, 4 April 1978, 78/80; Dorset, Lulworth, on *Laminaria digitata*, 3–5 m depth, 15 March 1983, 83/225; Devon, Wembury, on *Laminaria* drift, 5 December 1983, 83/490; Devon, Wembury, on *Laminaria digitata*, upper subtidal, 13 December 1985, 85/191; Dorset, Lulworth, on *Laminaria hyperborea* with *T. pustulatum* var. *pustulatum*, 1–2 m depth, 9 September 1986, 86/134; Devon, Wembury, on *Laminaria* drift, 24 November 1988, 88/123.

HERBARIUM SPECIMEN MISIDENTIFIED AS T. LAMINARIAE. As *Choreonema laminariae*, Norway, Kristiansund, *Foslie* (BM!) (= *T. pustulatum* var. *pustulatum*). Most published references (as *Lithophyllum (Dermatolithon) pustulatum* f. *laminariae*), since 1905 refer to var. *pustulatum* growing on *Laminaria* stipes and holdfasts.

GLOSSARY

The following definitions apply to their use in the context of this treatment of *Titanoderma*; an extended glossary is available in Woelkerling (1988: 225).

Apomictic: reproducing without karyogamy and meiosis.
Appressed: pressed together without being united.
Axial filament: any one of the unistratose, basal layer of thallus filaments (Figs 9–11, 50).
Basionym: the original name of a taxon.
Bisporangium: a sporangium whose contents divide mitotically (presumably) to form two diploid (presumably) bispores (Fig.23). Binucleate bispores have not been observed in this study.
Bistratose: composed of two layers.
Bulbous: type of conceptacle surface (Fig.48).
Columella: structure often occurring in the centre of the floor of a tetra/bisporangial conceptacle (Fig. 23).
Columnar cell: cell of erect filament which is relatively tall and narrow in VS (Fig. 14).
Concavity: depression on thallus or conceptacle surface formerly occupied by an epithallial cell (Fig. 37).
Conceptacle: an enclosed chamber which contains reproductive structures.
Conceptacle primordium: a group of meristematic cells from which a conceptacle develops.
Contiguous: adjacent, used particularly to describe the proximity of aligned cells from different filaments (Fig. 20).
Diagnostic characters: those characters that distinguish taxa of equal rank unequivocally.
Differential characters: those characters that collectively indicate distinctions between taxa of equal rank.
Dimerous: a type of thallus construction involving two sets of filaments (axial and erect) at right angles to one another.
Epilithic: growing attached to rock, stones, glass etc.
Epithallial cell: a cell formed outwardly from either an axial cell or a subepithallial initial (Fig. 50).
Epizoic: growing on animal substrata such as shells.
Erect filament: filament derived from, and at right angles to, an axial filament (Figs 11, 50).
Filament: a row of cells joined by primary pit connections (Figs 9, 11, 50).
Flat thallus: a thallus of generally flattened appearance lacking protuberances etc., cf. smooth thallus which applies to microscopic features.
Fusion cell: a cell formed after karyogamy, subsequently giving rise to gonimoblast filaments (Fig. 244).
Holotype: 1) the single specimen or other element designated in the protologue of a species by the original author to serve as the nomenclatural type; 2) the single specimen or other element used by an author in originally describing a species.
Honeycomb-like: type of conceptacle surface (Fig. 36).
Horseshoe-like: type of conceptacle surface (Fig. 46).
Hypothallial filaments: name sometimes used for axial filaments.
Imbricating: in which lobe-like parts of a thallus overgrow one another (Figs 154, 199).
Initial: a meristematic cell, cf. subepithallial, terminal initials.
Isolectotype: a duplicate of a lectotype specimen (q.v.).
Lateral: borne from the side of an axis.
Lectotype: a specimen from an author's original collection selected by a subsequent author to serve as the nomenclatural type.
Margin: The peripheral area of a dorsiventral thallus, often composed of axial and epithallial cells only and not usually bearing conceptacles.
Multistratose: composed of many layers.
Nomenclatural type: the single specimen or element of a taxon to which its name is permanently attached.
Ostiole: the pore in the roof of a conceptacle through which spores are discharged (Fig. 23).
Ostiole canal: the passage between an ostiole and a conceptacle chamber, most conspicuous when the conceptacle roof is thick (Fig. 141).
Palisade cell: cell of an axial filament which is relatively tall, narrow, and usually obliquely orientated in VS (Fig. 9).
Papillae: small swollen cells sometimes lining the ostiole canal (Fig. 105).
Perithallial filaments: name sometimes used for erect filaments.
Postigenous filaments: name sometimes used for erect filaments.
Primary pit connection: formed between two successive cells of a filament during cell division (Figs 9–11), cf. secondary pit connection.
Primigenous filaments: name sometimes used for axial filaments.
Prominent: (used of conceptacles) protruding markedly and abruptly from the thallus surface (Fig. 170), cf. raised.
Protologue: all the information associated with the original publication of a taxonomic name.
Raised: (used of conceptacles) protruding gradually somewhat above the thallus surface (Fig. 36), cf. prominent.
Ridged: type of conceptacle surface (Fig. 44).
Row: horizontally aligned contiguous cells of erect filaments.
Secondary pit connection: pit connection formed between two mature cells of contiguous axial or erect filaments (Figs 9–11), cf. primary pit connection.
Sinuate: with a wavy outline, used of axial cells (Fig. 9) and rows of erect filament cells (Fig. 66).
Smooth thallus: thallus surface lacking microscopic protrusions, flakes, etc. and therefore not roughened, cf. flat thallus which applies to macroscopic features.
Stepped: type of conceptacle surface (Fig. 40).
Subepithallial initial: situated subterminally on an erect filament cutting off epithallial cells outwardly and erect filament cells inwardly (Figs 9, 11, 50).
Terminal initial: situated terminally on an axial filament cutting off axial cells inwardly (Figs 9, 50).
Tetrasporangium: a sporangium whose contents divide meiotically (presumably) and simultaneously to form four zonately arranged haploid (presumably) tetraspores (Fig. 247).
Unistratose: composed of one layer.

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INDEX

Accepted names are in roman, synonyms in *italic*. New names and principal references are in **bold**. An asterisk (*) denotes a figure; if this occurs after a group of references (eg 33–49*) the figure, or figures, occur within the group, not necessarily on the page with the asterisk.

Acanthatylo heredia 33, 49
Amphiroideae 11
Amphiroa 11, 13, 69

Ceramiales 11
Ceramium rubrum 29, 33
Chondrus 7, 25, 31–33
  crispus 22, 26*, 29, 33, 69
Choreonema thuretii 13
  laminariae 33, 73, 75
Cladophora 25, 63
  pellucida 58, 64, 66
  rupestris 22, 28, 53*, 58, 61–64*, 66
Cladostephus spongiosus 30, 33
Clathromorphum reclinatum 21
Corallina 5, 25, 49, 55, 61, 64–69*
  officinalis 22, 26, 29, 53*, 58, 60, 61, 67, 69
Corallinaceae 11
Corallinales 11–13
Cryptacantha squarrosa 29, 33
Cystoseira baccata 69
  nodicaulis 22, 58

Dermatolithon 2, 5, 8–11, 22, 25, 29, 36, 60
  adplicitum 34, 49
  ascripticium 50, 52, 61
  canescens 16, 19
  confinis 50
  corallinae 16, 19, 66, 69
  crouanii 31, 70, 73, 75
  cystoseirae 55
  dispar 16, 19
hapalidioides 27*, 32–34, 36, 48, 49, 61
    f. *confinis* 50, 61
    f. *typica* 36
  laminariae 31, 69
  litorale 16, 19, 21, 50, 52, 55, 58, 61, 62, 64
  macrocarpum f. *faeroensis* 26, 29, 32
    f. *laminariae* 29, 31
  nodulosum 20
  polymorphum 33
  pustulatum 5, 21, 26, 31, 32, 62, 63
    f. *ascripticium* 50
    f. *crinita* 29
    f. *laminariae* 31–33, 73
    f. *macrocarpa (um)* 29, 33

f. *typica* 31
tumidulum 16, 19
Dumontia 13

Epilithon 8
pustulatum 26
Ezo 11, 13, 23

Fosliella 2, 4, 5, 9, 13, 16, 19–22, 29, 33, 61–63
acripticia 50
cruciata 60, 61
farinosa 58, 61, 66, 67
intermedia 50
Fucus 61
Fucus serratus 33, 61, 66
vesiculosus 52, 55, 61
Furcellaria 24–26, 55, 57, 58, 61, 66*
lumbricalis 22, 33, 53*, 54*, 56, 59*, 60*, 61, 67, 69

Gelidium 49, 55, 63
corneum 50
pusillum 22, 24, 25, 29, 53, 56*, 58, 61, 64, 69
Gigartina 28, 33
mamillosa 26, 33
Goniolithon 11, 23
Gymnogongrus crenulatus 33

Halopitys incurvus 22, 58, 61

Jania 25, 63
rubens 22, 64

Laminaria 24*, 25, 29–33*, 45, 73, 75
cloustonii 28, 33, 73, 75
digitata 7, 22, 33, 69, 70, 72, 73, 75
hyperborea 22, 28*, 33, 49, 75
Laurencia pinnatifida 22, 25, 54*, 58, 59*, 61, 69, 75
Leptophytum 21
Litholepis 9, 10, 22
caspica 10, 22, 23
Lithophylloideae 11–13, 16, 23
Lithophyllum 3, 8–11, 13, 16, 22, 23, 25, 29, 36, 50
corallinae 16, 19, 66
crouanii 16, 22, 26, 28, 29, 31–33, 72, 75
hapalidioides 12*, 34, 34*, 36, 49
f. *confinis* 50
incrustans 13, 45*
intermedium 52
lichenoides 10, 11
litorale 16, 19, 50, 52, 55, 60, 61
macrocarpum 26, 29, 33, 36, 61
f. *corallinae* 66
f. *faeroensis* 29
f. *intermedia (um)* 50, 52, 55, 61
f. *laminariae* 69, 75
orbiculatum 31, 72
pustulatum 26, 29, 31, 33, 34, 36, 41*, 48, 49, 62
f. *ascripticia (um)* 29, 50, 52
f. *australis* 10
f. *corallinae* 29, 66
f. *faeroense (is)* 26, 29, 33*
f. *intermedia* 4, 29, 50, 51*, 52, 53, 60*, 61, 62
f. *laminariae* 31, 69, 75
var. *laminariae* 26, 28, 31
f. *macrocarpa (um)* 26, 34, 52
f. *similis* 29
Lithoporella 13
Lithothamnion 3
adplicitum 4, 34, 36, **42–43***, 44, 46*, 48
stromfeltii f. *tenuissima* 36, 49
Littorina 58, 59*, 61
Lithothrix 11, 13
Lomentaria articulata 58–61*

Mastocarpus 25, 31, 32
stellatus 22, 26, 29, 33
Mastophoroideae 16
Melobesia 4, 5, 8, 9, 22, 25, 36
canellata 62
confinis 4, 5, 7, 8*, 49–53*, 59*, 61
corallinae 4, 5, 7, 64*, 66–68*, 69
discoidea 63
farinosa 5, 7, 61, 63
hapalidioides 4, 6*, 7, 18*, 34*, 35*, **36–40***, 44, 48, 50, 61
f. *confinis* 69
laminariae 4, 7, 31, 69, 70*, 72, 73, 75
lithothamnioides 70*, 70, 72, 73
macrocarpa 7*, 7, 26, 29, 33–36, 48, 55
membranacea 5, 7, 8, 25, 26*, 28*, 30, 33, 53*, 58, 62, 66*, 69, 73, 75
orbiculata 5
pustulata 5, 7–11, 25, 26, 29, 33, 49, 62
β *canellata* 4, 5, 29, 33, 61, 66
simulans 4, 7, 34, 36, **40–42***, 43, 46*, 48, 49
verrucata (um) 5, 7, 17*, 61–63, 66, 69
Mesophyllum lichenoides 69
Metamastophora 3, 4
flabellata 4
Millepora 4
tortuosa 4, 8, 10
undulosa 4
Neogoniolithon 3
Nitophyllum ruprechtianum 50

Ostrea 61

Padina 63
Palmaria 61, 66
palmata 33, 53*, 61, 69, 75
Patella 33, 49, 50, 53*
Pholas 34, 42
Phymatolithon 28, 33
laevigatum 20
lenormandii 20, 22, 53, 58, 73
Phyllophora 24, 26, 33, 36, 48, 49, 61
crispa 22, 33*, 49
pseudoceranoides 33, 49
rubens 26, 34, 49, 66
Pneophyllum 2, 4, 7, 9, 10, 13, 16, 19–22, 60, 63, 66
limitatum 29, 58, 61–63, 66
microsporum 58
Polysiphonia 16, 69
elongata 22
nigrescens 69
Posidonia 36
Pseudolithophyllum 13
Pterocladia capillacea 69

Rytiphlo(a)ea 7, 61, 62

Sargassum linifolium 29, 33
muticum 58
Sporolithon 11

Tenarea 4, 5, 8, 10, 11, 23
acripticia 50
canescens 69
confinish 50
corallinae 66, 69
hapalidioides 34, 36, 49
pustulata 26
tortuosa 10, 11
tumidulum 69
undulosa 10, 11
Titanoderma 2–11, 13–20* (structure), **22–24**, 20–75 (British Isles species)
confine (is) 50
corallinae 4, 6*, 8*, 13, 18–22, 24*, 25, 29, 53*, 58, 60, **64–69***
hapalidioides 34
laminariae 4, 18, 20–22, 24–26*, 28, 29, 31–33, 67, **69–75***
litorale 50
macrocarpum 34, 36
prototypum 6*, 13, 20
pustulatum 4, 7, 11, 13, 18, 20–22, 25, 26, 69
var. **canellatum** 5, 7, 13, 17*, 20–25*, 29–31, 33, 52, 53*, 58, **61–66***
var. **confine** 8*, 10, 12*, 16–26*, 29–31, **49–61***, 66, minute form 56*, **57–58***, 64, 69
var. **macrocarpum** 5–8*, 14*, 16, 18*, 18, 21–26*, 29, 32, **33–49***, imbricating form 47–50*, 55, 67
var. **pustulatum** 5–7*, 9*, 10*, 12–16*, 18, 21–24, **26–33***, 48, 55, 62, 67, 73, 75
tessellatum 13
verrucatum 61

Zostera 61

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